Fisheries and Oceans Canada | Pêches et Océans Canada
Ecosystems and Oceans Science | Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2016/101

Central and Arctic Region

Modelling Survival and Establishment of Grass Carp, *Ctenopharyngodon idella*, in the Great Lakes Basin

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January 2017

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

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ISSN 1919-5044

Correct citation for this publication:

Jones, L.A., Drake, D.A.R., Mandrak, N.E., Jerde, C.L., Wittmann, M.E., Lodge, D.M., van der Lee, A.S., Johnson, T.B., and Koops, M.A. 2017. Modelling Survival and Establishment of Grass Carp, *Ctenopharyngodon idella*, in the Great Lakes Basin. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/101. vi + 52 p.

TABLE OF CONTENTS

ABSTRACT V

RÉSUMÉ VI

GENERAL INTRODUCTION 1

1.0 BIOENERGETICS MODELLING OF POTENTIAL GROWTH AND CONSUMPTION BY GRASS CARP IN THE GREAT LAKES 2

- ABSTRACT 2
- INTRODUCTION 2
- METHODS 3
  - The model 3
  - Parameterization 5
  - Simulation 7
  - Sensitivity analysis 8
- RESULTS 9
  - Model sensitivity 14
- DISCUSSION 15
  - Uncertainties 17
  - Interpretation 18
- CONCLUSION 19

2.0 EVALUATING THE NET REPRODUCTIVE VALUE OF GRASS CARP IN THE GREAT LAKES FOR POTENTIAL ESTABLISHMENT 19

- INTRODUCTION 19
- METHODS 20
  - Estimating the net reproductive value 20
  - Parameter values 22
  - Age of reproductive maturity 23
  - Management Scenarios 24
  - Matrix population modeling 25
- RESULTS 26
  - Estimating the net reproductive value 26
  - Age of reproductive maturity 26
  - Management scenarios 27
  - Matrix population model 28
- DISCUSSION 28

3.0 SIMULATION OF OVERWINTER SURVIVAL OF FIRST-YEAR GRASS CARP *CTENOPHARYNGODON IDELLA* IN THE GREAT LAKES BASIN 30

- ABSTRACT 30
- INTRODUCTION 30
- METHODS 32
- RESULTS 36

Lake Superior 42
Lake Huron 42
Lake Michigan 42
Lake Erie 42
Lake Ontario 43
Basin-wide sensitivity analysis 43
CONCLUSION 43
GENERAL CONCLUSIONS 44
REFERENCES CITED 44
APPENDIX 1: DISTRIBUTION OF GRASS CARP INTO SUITABLE STREAMS 51

ABSTRACT

Grass Carp (*Ctenopharyngodon idella*), is a large, herbivorous fish that was first introduced to North America in 1963 for aquatic macrophyte control. It has since escaped from where it was stocked and entered rivers of the central United States and has dispersed through the Mississippi River basin towards the Great Lakes. Commerce is also another source of spread in the United States, where sale of diploid and certified triploid (reproductively sterile) Grass Carp is legal in several states. Between 2007 and 2012, 45 Grass Carp were known to have been caught in the Great Lakes basin, raising concerns that a sufficient number of individuals are present and may be able to form a self-sustaining population. The potential for Grass Carp to invade the Great Lakes is of increasing concern and there is a management need to understand the probability of introduction and the potential ecological consequences of Grass Carp to the Great Lakes basin. Three modelling approaches were used to inform the likelihood of Grass Carp survival and establishment in the Great Lakes basin.

First, a bioenergetics model is presented to assess the likelihood of Grass Carp survival. Model results predicted growth and survival in the Great Lakes is possible using a variety of diets including solely *Cladophora* spp. A reproductive-sized Grass Carp weighing approximately 3 kg required approximately 15 kg of macrophytes annually to maintain body weight. This is likely achievable based on mean macrophyte biomass estimated in different regions of the Great Lakes. The potential loss of macrophytes from individual consumption pressure could be amplified if feeding preference or foraging behaviour result in plant damage beyond what is consumed (e.g., shifting macrophyte composition). The second modelling approach used the net reproductive value to assess the potential for establishment in the Great Lakes basin. The net reproductive rate (R_0) for Grass Carp in the Great Lakes was 24.8, indicating that Grass Carp are likely to establish in the Great Lakes. Varying the model to include slower maturation times for reproduction yields the same result of successful establishment. Third, a stochastic model was used to predict the overwinter survival of young-of-year (YOY) Grass Carp to estimate the likelihood of establishment. Overwinter mortality of YOY ranged from 0.42 to 1.0, with 100% mortality in more northern locations within the Great Lakes. These modelling approaches predict that Grass Carp has the potential to survive and establish in the Great Lakes basin.

Modélisation de la survie et de l'établissement de la carpe de roseau, *Ctenopharyngodon idella*, dans le bassin des Grands Lacs

RÉSUMÉ

La carpe de roseau (*Ctenopharyngodon idella*) est un grand poisson herbivore qui a été introduit pour la première fois en Amérique du Nord, en 1963, pour le contrôle des macrophytes aquatiques. Depuis, des individus se sont échappés d'où ils vivaient, ont franchi les rivières du centre des États-Unis, puis se sont dispersés aux quatre coins du bassin du fleuve Mississippi. Ils ont ensuite gagné les Grands Lacs. Le commerce est autre facteur à l'origine de cette propagation aux États-Unis, car la vente d'individus diploïdes et triploïdes certifiés (stériles) de carpe de roseau est légale dans plusieurs États. On sait que, entre 2007 et 2012, 45 individus ont été capturés dans le bassin des Grands Lacs. Ainsi, on craint de plus en plus qu'il y ait suffisamment d'individus présents, et que ceux-ci soient à même de former une population autosuffisante. La possibilité que la carpe de roseau envahisse les Grands Lacs est une préoccupation croissante, et la direction doit comprendre la probabilité d'introduction et les conséquences écologiques possibles de la présence de la carpe de roseau dans le bassin des Grands Lacs. On a utilisé trois approches de modélisation afin de connaître la probabilité que la carpe de roseau s'établisse et survive dans le bassin.

D'abord, on présente un modèle bioénergétique, afin d'évaluer la probabilité de survie de la carpe de roseau. Les résultats du modèle prévoient qu'une croissance et une survie dans les Grands Lacs sont possibles au moyen de divers régimes, notamment par la consommation d'espèces de *Cladophora*. Une carpe de roseau ayant atteint la maturité sexuelle et qui pèse environ 3 kg a besoin d'environ 15 kg de macrophytes par année pour maintenir son poids. La biomasse de macrophytes moyenne mesurée dans les diverses régions des Grands Lacs démontre que cette éventualité est très probable. La perte éventuelle de macrophytes découlant de la pression issue de la consommation des individus pourrait augmenter, si cette préférence alimentaire ou le comportement de recherche de nourriture entraîne une dégradation des plantes, alors surconsommées (p. ex., changement dans la composition des macrophytes). Avec la deuxième approche de modélisation, on a utilisé la valeur reproductive nette pour évaluer la probabilité que l'espèce s'établisse dans le bassin des Grands Lacs. Le taux de reproduction net (R_0) de la carpe de roseau dans les Grands Lacs était de 24,8, ce qui indique qu'il est probable que l'espèce s'y établisse. Si l'on modifie le modèle, en y mettant des temps de maturation sexuelle plus longs, on obtient le même résultat, à savoir un établissement réussi. Comme troisième approche, on a utilisé un modèle stochastique. On s'en est servi pour prédire le taux de survie hivernale des jeunes de l'année de la carpe de roseau, pour pouvoir évaluer la probabilité d'un établissement. Le taux de mortalité hivernale des jeunes de l'année va de 42 % à 100 %. Dans les endroits les plus nordiques des Grands Lacs, ce taux est de 100 %. Ces approches de modélisation révèlent qu'il est possible que la carpe de roseau s'établisse et survive dans le bassin des Grands Lacs.

GENERAL INTRODUCTION

Grass Carp (*Ctenopharyngodon idella*), one of the four species of Asian carps, is a sub-tropical to temperate species native to the large rivers of eastern Asia. Grass Carp was originally brought to North America in 1963 to evaluate their potential for biological control of aquatic vegetation. By the late 1970s, concern about the ability of Grass Carp to reproduce and cause ecological damage in large rivers led many states to ban the introduction of reproductively viable Grass Carp (Leslie et al. 1996). However, stocking of diploid (fertile) and triploid (functionally sterile) Grass Carp remains legal in some states. Grass Carp are currently established throughout the Mississippi River basin of the United States and recent captures of diploid Grass Carp in the Great Lakes basin have raised concerns that a sufficient number of individuals are present to form a self-sustaining population (Wittmann et al. 2014).

An earlier risk assessment of Asian carps, which included Grass Carp, identified broad potential risks to Canada, including the Great Lakes (Cudmore and Mandrak 2004). While this risk assessment provided insight into the risk faced by broad areas of Canada, knowledge gaps were identified as a result of the lack of information. Given this, and the recent discovery of Grass Carp recruitment in Lake Erie (Chapman et al. 2013), an ecological risk assessment of Grass Carp to the Great Lakes basin was proposed by Fisheries and Oceans Canada (DFO) and the Great Lakes Fishery Commission (GLFC) to the Asian Carp Regional Coordinating Committee (ACRCC) and was endorsed in early 2014.

The purpose of this research document was to support the risk assessment by addressing some of the key concerns of a biological invasion which include the ability of Grass Carp to survive and establish. Several modelling approaches were used to address these concerns and to answer the following questions on the likelihood of Grass Carp survival and establishment in the Great Lakes basin:

1) Can Grass Carp grow and survive in the Great Lakes basin?

2) Can Grass Carp establish a viable population in the Great Lakes basin?

3) Can young-of-year (YOY) Grass Carp overwinter in the Great Lakes basin?

This document is structured into three sections, each addressing one of the aforementioned questions. First (question 1, Section 1.0), a bioenergetics model was used to assess the likelihood of survival, by estimating the amount of food consumed to support a specified growth rate. The model also predicts the amount of growth expected for a given level of consumption. Second (question 2, Section 2.0), a modelling approach used the net reproductive value to assess the potential for establishment in the Great Lakes basin. Finally (question 3, Section 3.0), a stochastic model was used to predict the overwinter survival of YOY Grass Carp to help inform the likelihood of establishment.

1.0 BIOENERGETICS MODELLING OF POTENTIAL GROWTH AND CONSUMPTION BY GRASS CARP IN THE GREAT LAKES

Adam S. van der Lee, Timothy B. Johnson, and Marten A. Koops

ABSTRACT

Grass Carp (*Ctenopharyngodon idella*) threatens to invade the Great Lakes and pose a substantial threat to native macrophytes. We address the potential for growth and survival of Grass Carp in the Great Lakes by developing a bioenergetics model parameterized through the primary literature. It is likely that young Grass Carp will have sufficient growth for winter survival and be able to reach reproductive size using a variety of diets, including solely *Cladophora* spp. Consumption by large adults could be up to 90 kg of macrophytes annually. These impacts could be amplified if feeding preference or foraging behaviour result in plant damage beyond what is consumed. There is, however, much uncertainty in the model outputs due to data limitations and high parameter sensitivities. These uncertainties pertain primarily to precise consumption/impact values rather than the more general conclusions of positive growth and survival.

INTRODUCTION

Grass Carp threatens to invade the Great Lakes and may already be reproducing naturally in the Great Lakes basin (Chapman et al. 2013). Consequently, it is important to determine how well Grass Carp will survive and grow in the Great Lakes and the potential extent of their impact. One method that can provide insight into these questions is bioenergetics modelling. Bioenergetics models are based on the energy balance equation where consumed energy is balanced by the costs of metabolism, growth and waste (Hanson et al. 1997). Typically these models are used to estimate the amount of food consumed to support a specified growth rate but can also predict the amount of growth expected for a given level of consumption.

Previously, bioenergetics models have been used to assess the potential for survival and impacts of other Great Lakes invaders such as Silver Carp (*Hypophthalmichthys molitrix*) and Bighead Carp (*H. nobilis*) (Cooke and Hill 2010, Anderson et al. 2015) and Round Goby (*Neogobius melanostomus*; Lee and Johnson 2005). Cooke and Hill (2010) matched energy requirements of Silver Carp and Bighead Carp to the availability of phytoplankton and zooplankton and concluded that under specific temperature and activity regimes these species will struggle to survive in many open water areas in the Great Lakes. Anderson et al. (2015) provided an update and concluded these carps will not be food limited in Lake Erie. Lee and Johnson (2005) developed a bioenergetics model for Round Goby, which invaded the Great Lakes in the early 1990s (Charlebois et al. 1997). Round Goby is primarily a benthivore and could act as a vector for material transfer between the benthic and pelagic zones. As a result, their bioenergetics model can be used to quantify the flow of energy, contaminants, and nutrients from the benthic to pelagic environments and the associated impacts to piscivorous fishes (Lee and Johnson 2005).

As a primarily herbivorous species Grass Carp is fairly unique among fish species. Grass Carp has proven to be voracious consumers of plant material and has been widely introduced throughout the world for aquatic weed control (Pípalová 2006). Grass Carp do exhibit a preference for certain plant species (Wiley et al. 1986, Pine and Anderson 1991) likely related to the handling time required for consumption (Dibble and Kovalenko 2009) and independent of caloric content (Wiley et al. 1986). Food preference may also be related to macrophyte chemical composition (Bonar et al. 1990). Consumption rate increased with calcium content possibly because it is required for growth and decreased with cellulose content likely due to handling

time (Bonar et al. 1990). Grass Carp, especially young individuals, will accept animal product as part of their diet (Fedorenko and Fraser 1978) and animal product may be required for positive growth for young juveniles (Fischer 1973); although wild Grass Carp will generally feed almost exclusively on macrophytes from approximately one month after hatching (Cudmore and Mandrak 2004).

We develop a bioenergetics model for Grass Carp in an environment representative of the Great Lakes, specifically Lake Erie, based on the Wisconsin model (Hanson et al. 1997). We parameterized the model using values derived from the primary literature and attempted to address a number of questions relating to Grass Carp invading the Great Lakes:

1) Will young-of-year (YOY) be able to exhibit positive growth sufficient to survive the first winter?;
2) How well will Grass Carp grow/survive if they feed exclusively on *Cladophora* spp.?;
3) What is the consumptive pressure exerted by Grass Carp of different sizes/stages on aquatic vegetation?; and,
4) How much food is required for adult Grass Carp to maintain their body mass?

METHODS

The model

We modelled Grass Carp bioenergetics using the principles of the Wisconsin model (Hanson et al. 1997) where annual growth, ΔB (g_{fish} y^{-1}), is:

$$\Delta B = \sum_{i=1}^{365} \left([C_i - (R_i + S_i + F_i + U_i)] \frac{E_{prey}}{E_{fish}} W_i \right) - GW_s \qquad (1)$$

Where i is day of year, C is the daily per gram consumption of food, R is respiration or the per gram cost of metabolism, S represents the per gram cost of specific dynamic action, F is the per gram losses to egestion and U is the excretion or the per gram losses due to nitrogenous waste. Each of these variables are in units of g_{prey} g_{fish}^{-1} d^{-1} and must be converted to units of g_{fish} g_{fish}^{-1} d^{-1} through the ratio of energy densities of the prey, E_{prey}, and Grass Carp, E_{fish}. W is the current weight (g) of the fish and G represents gonad production, which is calculated as a proportion of body weight the day of spawning, s. Values related to variable estimates are listed in Table 1.1.

Daily consumption rate (g_{prey} g_{fish}^{-1} d^{-1}) was a function of body size and temperature:

$$C = p \cdot a_C W^{-b_C} f_C(T) \qquad (2)$$

where, $f_C(T)$ is the temperature-dependent function with temperature, T, in °C, a_C and b_C are the intercept and slope of the allometric function (Table 1.1), and p is a proportional value to scale laboratory estimates of maximum consumption with ad *libitum* feeding to more natural rates.

Table 1.1. Summary of parameter values used in the bioenergetics Grass Carp model. Allometric parameter values differ between prey-independent (PIC) and prey-dependent consumption (PDC) forms.

Symbol	Description	Value		Source
		PIC	PDC	
a_C	Intercept of allometric consumption function	$1280.82/E_{prey}$	1.8955	Fischer (1973)
b_C	Coefficient of allometric consumption function	0.2979	0.374	Fitted
te_1	Temperature for xk_1 (°C)	8		Cudmore and Mandrak (2004)
te_2	Temperature for xk_2 (°C)	22		Fedorenko and Fraser (1978)
te_3	Temperature for xk_3 (°C)	30		Kilambi and Robison (1979)
te_4	Temperature for xk_4 (°C)	35		Wiley and Wike (1986)
xk_1	Proportion of C_{max} at te_1	0.15		This analysis
xk_2	Proportion of C_{max} at te_2	0.98		This analysis
xk_3	Proportion of C_{max} at te_3	0.98		This analysis
xk_4	Proportion of C_{max} at te_4	0.05		This analysis
a_R	Intercept of allometric respiration function	0.0019		Cui et al. (1994)
b_R	Coefficient of allometric respiration function	0.3364	0.339	Fitted
c_R	Temperature coefficient for respiration	0.43		Wiley and Wike (1986)
a_S	Coefficient for specific dynamic action	0.07		Carter and Brafield (1992); Wiley and Wike (1986)
a_F	Proportion of consumed food egested	0.5		Van Dyke and Sutton (1977); Cui et al. (1994)
a_U	Proportion of food excreted	0.076		Cui et al. (1992)
E_{fish}	Energy density of Grass Carp	4874		Scott and Orr (1970); Hadjinikolova et al. (2008)
E_{prey}	Approximate energy density of prey source	900 (duckweed); 1350 (*Cladophora*); 2250 (*Elodea*);		Fischer (1968); Paine and Vadas (1969); Wiley and Wike (1986)
T_{max}	Maximum temperature	26		This analysis
T_{max}	Minimum temperature	2		This analysis
d_{Tmax}	Day of maximum temperature	225		This analysis
Wp	Duration of winter plateau in temperature	50		This analysis

Temperature-dependence was modelled using equation 3 described in the Wisconsin model (Thornton and Lessem 1978). This form is appropriate for cool- and cold-water species and is the product of two logistic curves (ascending and descending) resulting in a dome-shaped relationship:

$$f_C(T) = \frac{xk_1 e^{f1(T-te_1)}}{1+xk_1(e^{f1(T-te_1)}-1)} \cdot \frac{xk_4 e^{f2(te_4-T)}}{1+xk_4(e^{f2(te_4-T)}-1)} \quad (3)$$

$$f1 = \frac{1}{te_2-te_1} ln\left[\frac{xk_2(1-xk_1)}{xk_1(1-xk_2)}\right] \quad (4)$$

$$f2 = \frac{1}{te_4-te_3} ln\left[\frac{xk_3(1-xk_4)}{xk_4(1-xk_3)}\right] \quad (5)$$

This function takes eight input parameters: four temperatures and four corresponding proportional values (Table 1.1). The parameters te_2 and te_3 correspond to the plateau region where consumption is close to maximal and te_1 and te_4 are the thermal limits where consumption rates are very low.

Metabolic rate is a product of standard (resting and unfed) respiration rate (a function of body size and temperature), activity level, and specific dynamic action (the energy cost of food digestion). The respiration portion of metabolism was modelled as:

$$R = a_R W^{-b_R} \cdot e^{c_R T} \cdot ACT \cdot \frac{E_{oxy}}{E_{prey}} \quad (6)$$

where a_R and b_R represent the intercept and slope of the allometric function for respiratory costs, c_R is the coefficient of temperature dependence, ACT is the activity level, E_{oxy} is the oxy-calorific coefficient (13556 J g_{O2}^{-1}), and E_{prey} is the energy density of prey (Table 1.1). The specific dynamic portion of metabolism was modelled as a proportion of assimilated energy, a_S:

$$S = a_S(C - F) \quad (7)$$

Waste represents the loss of energy due to egestion of feces, F, and excretion of nitrogenous wastes, U, which were modelled as a constant proportion of consumption, a_F, and assimilation, a_U, respectively:

$$F = a_F C, \quad (8)$$
$$U = a_u(C - F) \quad (9)$$

Parameterization

An important consideration in parameterizing a bioenergetics model is a reasonable outcome under ideal conditions (a p-value of 1); a reasonable outcome being a fish growing at a rate and attaining a maximum size that is possible for the given species. With this criterion we parameterized the Grass Carp bioenergetics model using relationships from the primary literature. Best fit parameters were those that produced a fish between 75 and 100 kg at age 10 (approximately twice the maximum reported size in the wild; Froese and Pauly 2014) with fish reaching size of maturity corresponding to age 3 and older. Preliminary analysis and previous bioenergetics model sensitivity analysis (Bartell et al. 1986) have shown the allometric exponent of consumption (b_C, equation 2) and respiration (b_R, equation 6) to be the most sensitive and were therefore the parameters we varied to meet our "reasonable growth" criteria. We defined the possible range of parameter values for the two exponents from the primary literature and iteratively tested all possible combinations with 0.005 increments. The consumption exponent was varied between 0.19 (Fischer 1973) and 0.50 (Fischer 1970) and the respiration exponent was varied between 0.24 (Stanley 1974) and 0.355 (Wiley and Wike 1986). The combinations that satisfied the above criteria were averaged and used in simulations (Table 1.1).

Grass Carp daily consumption is expected to be high with reports of consumption rates greater than 100% of body weight per day (Fedorenko and Fraser 1978, Wattendorf and Anderson 1984, Osborn and Riddle 1999); however, few researchers have explored the relationship between consumption and body size. Fischer (1973) measured Grass Carp consumption for individuals ranging in size from 15–450 g and fed a diet of lettuce (*Lactuca sativa*). The results were reported as a daily caloric intake and can be interpreted two ways:

1) daily consumption is dependent on the prey species' energy content and growth will be independent of prey species;

2) daily consumption will be independent of prey species' energy content with growth differing with prey species.

We tested the effects of both these assumptions using two different consumption intercept values and, as a result, two different consumption and respiration exponent values (Table 1.1). We refer to the respective consumption relationships as prey-independent consumption (PIC) and prey-dependent consumption (PDC).

For the effect of temperature on consumption we chose a low consumption level below 8 °C because consumption has been found to effectively cease below this value (Cudmore and Mandrak 2004). Steady consumption starts between 10–16 °C (Shireman and Smith 1983) and has been found to more than double between 20 and 22 °C (Fedorenko and Fraser 1978). We therefore chose 22 °C as the point where consumption nears maximum. Kilambi and Robison (1979) found no significant difference in consumption rates between 18 and 30 °C; consequently, we choose the latter value (30 °C) as the threshold where consumption begins to decrease. Finally, for the high temperature at which consumption almost ceases we chose 35 °C which is near the thermal maximum of Grass Carp (38 °C; Cudmore and Mandrak 2004).

Many allometric relationships for Grass Carp respiration are available in the primary literature (e.g., Fischer 1970, 1973, Stanley 1974, Wiley and Wike 1986); however, few represent the standard metabolic rate. As a result, for the intercept value (a_R) we chose the value (rescaled to 0 °C) from Cui et al. (1993, 1994) which represents the respiration of an unfed, stationary individual. This value was less than all others representing routine metabolism and was consistent with other estimates of Grass Carp respiration (Yan et al. 2012). The temperature effect was taken from Wiley and Wike (1986) and refit as an exponential. ACT is a scalar multiplier to account for the additional cost of movement. Activity costs are expected to be relatively low for Grass Carp with average daily distances travelled generally less than 200 m d^{-1} (Clapp et al. 1993, Olive et al. 2010, Stich 2011). In experiments, oxygen consumption rates were between 2 and 5 times resting rates at maximum activity levels (Fu et al. 2009, Yan et al. 2012, Cai et al. 2014) where swim speeds were often higher than would be expected under natural circumstances. Respiratory costs are converted from g_{O2} g_{fish}^{-1} d^{-1} to g_{prey} g_{fish}^{-1} d^{-1} through the ratio of E_{oxy} and E_{prey}. Carter and Brafield (1992) estimated specific dynamic action to be 7% of absorbed energy when on a duckweed diet (*Lemna* sp.).

For a herbivore, Grass Carp has a short gut (Fedorenko and Fraser 1978) and is a poor digester of plant matter. Consequently, assimilation is expected to be low, generally less than 50% (Fedorenko and Fraser 1978) and can be as little as 20% (Fischer 1973, Fedorenko and Fraser 1978). Estimates of egestion vary widely with low estimates of roughly 35% of consumption (Cui et al. 1992) and high estimates of 87% (Fischer 1972). We use an intermediate estimate of 50% (van Dyke and Sutton 1977, Cui et al. 1994) based on a duckweed diet. Measured excretion values range from 6.4 to 8.8% of assimilation when given a natural plant diet (Fischer 1972, Cui et al. 1992, 1994). We chose the value reported by Cui et al. (1992) of 7.6%.

The energy density (E_{fish}) of Grass Carp is likely related to diet and living conditions (Fischer and Lyakhnovich 1973). Values for age-1 fish ranged from approximately 3560 to 5415 J g^{-1} (Fischer and Lyakhnovich 1973). Scott and Orr (1970) and Hadjinikolova et al. (2008) measured the energy density of 33 g and 933 g Grass Carp respectively as 4864 and 4884 J g^{-1}. We use a value of 4874 J g^{-1} as the energy density of Grass Carp.

Simulation

We simulated annual growth of Grass Carp beginning 1 July until 30 June of the following year. Daily temperature (°C; Figure 1.1) is estimated using a modified sine wave which allowed for an extended winter period that is assumed to be a constant temperature.

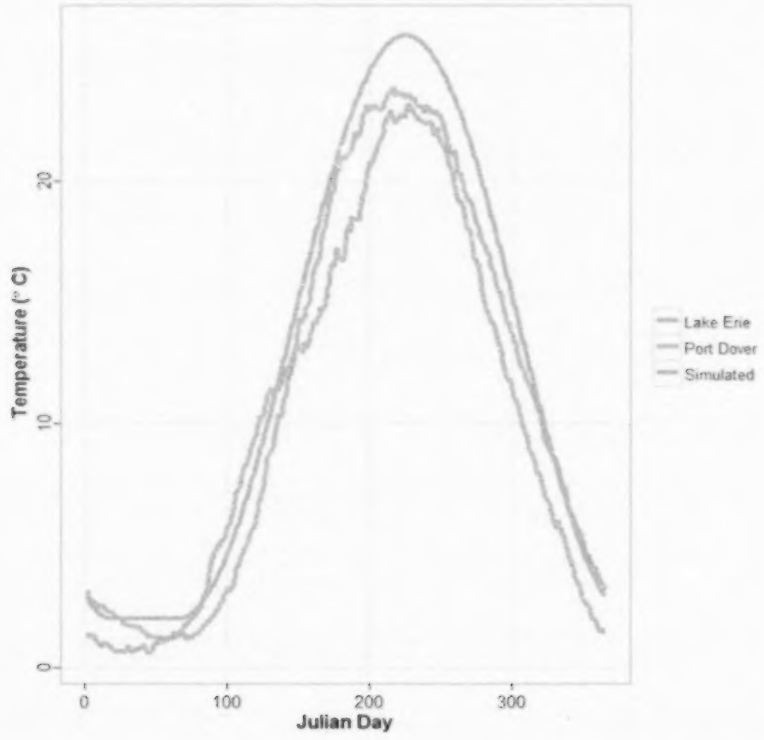

*Figure 1.1. Simulated daily temperature experiences by Grass Carp (*Ctenopharyngodon idella*) in the Great Lakes. Observed temperature for Port Dover and the average surface temperature for Lake Erie are included for reference.*

The function variables are: maximum temperature (T_{max}), minimum temperature (T_{min}), the day of maximum temperature (d_{Tmax}), and the duration of the winter plateau period (W_p) (Table 1.1). Daily temperature is estimated as:

$$T_d = \begin{cases} \left(\frac{T_{max}}{2} - 0.5T_{min}\right) \cdot \left(sin\left(\frac{2\pi\left(\left(d+\frac{Wp}{2}\right)-\left(d_{Tmax}-\frac{Wp}{2}-0.25(365-Wp)\right)\right)}{(365-Wp)} \right) + 1 \right) + T_{min} & From\ 1\ Jan\ to\ Wp \\ T_{min} & During\ winter\ plateau \\ \left(\frac{T_{max}}{2} - 0.5T_{min}\right) \cdot \left(sin\left(\frac{2\pi\left(\left(d-\frac{Wp}{2}\right)-\left(d_{Tmax}-\frac{Wp}{2}-0.25(365-Wp)\right)\right)}{(365-Wp)} \right) + 1 \right) + T_{min} & Following\ Wp \end{cases} \quad (10)$$

Parameter values were based on comparisons to Lake Erie daily average surface water temperature available from the NOAA Coastwatch website and temperature logger data from a water intake in Port Dover (Y. Zhao, Ontario Ministry of Natural Resources and Forestry (OMNRF), unpubl. data; Figure 1.1). The intake is located 457 m from shore, 2.74 m below the water surface, where the water depth is 4.57 m. We increased the maximum temperature by 2 °C based on the expectation that wetland areas inhabited by Grass Carp will likely have a slightly higher temperature than lake wide surface temperatures. Additionally, we chose to maintain a constant and slightly higher winter temperature (2 °C) based on the assumption that Grass Carp will be able to leave cooler areas for deeper waters. The overwinter temperature had little effect on model results.

We varied p from 0.01–1 to find a value corresponding to reasonable levels of growth for a variety of sizes (15, 250, and 5000 g, roughly equivalent to fish aged 0, 1, and 4), activity levels (2 to 5), food source energy densities (900, 1350, and 2250 J g^{-1}), and no spawning. The food energy densities correspond to preferred prey sources or those likely to be abundantly available in the Great Lakes. The 900 and 2250 J g^{-1} are approximately representative of duckweed (*Lemna* sp.) and *Elodea canadensis* which are low and high energy content examples of preferred food sources (Wiley and Wike 1986, Cudmore and Mandrak 2004). The 1350 J g^{-1} value is representative of *Cladophora* spp. which is abundant in the Great Lakes and a possible alternative food source when macrophytes are scarce. We define the expected level of growth as one where growth accounts for between 5 and 20% of the annual energy budget which is consistent with observed patterns in the laboratory (Haniffa and Venkatachalam 1980, Wiley and Wike 1986, Cui et al. 1992, 1994).

As an example of a potential Grass Carp life cycle, an additional simulation was run where growth was matched to a growth curve by iteratively adjusting the p-value annually until the specified weight is matched. Grass Carp growth was defined by a von Bertalanffy growth curve and converted to weights using relationships from FishBase (Froese and Pauly 2014):

$$L_t = 115.94(1 - e^{-0.23(t+0.16)}) \quad (11)$$

$$W_t = 0.016 L_t^{2.97} \quad (12)$$

Growth and consumption were estimated for fish of age-1 to age-16 starting on 1 July. For base simulations, we used a constant activity level of 2.5 and a prey energy density of 1350 J g^{-1}. Maturation occurs when an individual reaches 3 kg in weight (Shireman and Smith 1983). Spawning occurs once annually and can take place after 633 degree days of temperatures greater than 15 °C (Kocovsky et al. 2012) have been accumulated (starting from 1 January). We assumed that Grass Carp undertake a spawning migration lasting 14 days, with no feeding (Fedorenko and Fraser 1978) and a high activity level (5), and that gonad production (G) is 15% of body weight (Shireman and Smith 1983). An additional simulation was run to estimate the consumption necessary to maintain body mass over the course of a year. For this simulation no spawning activity was included.

Sensitivity analysis

Each parameter in the model (Table 1.1), excluding xk_1, xk_2, xk_3, and xk_4, was varied ± 10% while holding all other parameters constant to determine the influence of each on growth (final weight) and annual consumption. The sensitivity of growth was tested by holding p constant at 0.5 and allowing final weight to vary, while the sensitivity of consumption was tested by holding final weight constant and allowing p to vary. For each simulation an initial body size equivalent to an age-2 fish (1335 g), prey energy density of 1350 J g^{-1} and an activity level of 2.5 were used. All analyses were conducted using R 3.0.3 (R Core Team 2014).

RESULTS

We estimated a realistic range of growth and consumption possible using both the prey-independent consumption (PIC; Figure 1.2 and 1.3) and prey-dependent consumption (PDC; Figure 1.4 and 1.5) for a variety of prey sources, activity levels, and p-values for fish of sizes roughly equivalent to ages 0, 1 and 4 based on the von Bertalanffy growth function (Equation 11). Likely growth is defined as growth that constitutes 5 to 20% of the annual energy budget (highlighted as the thick portion of the curves).

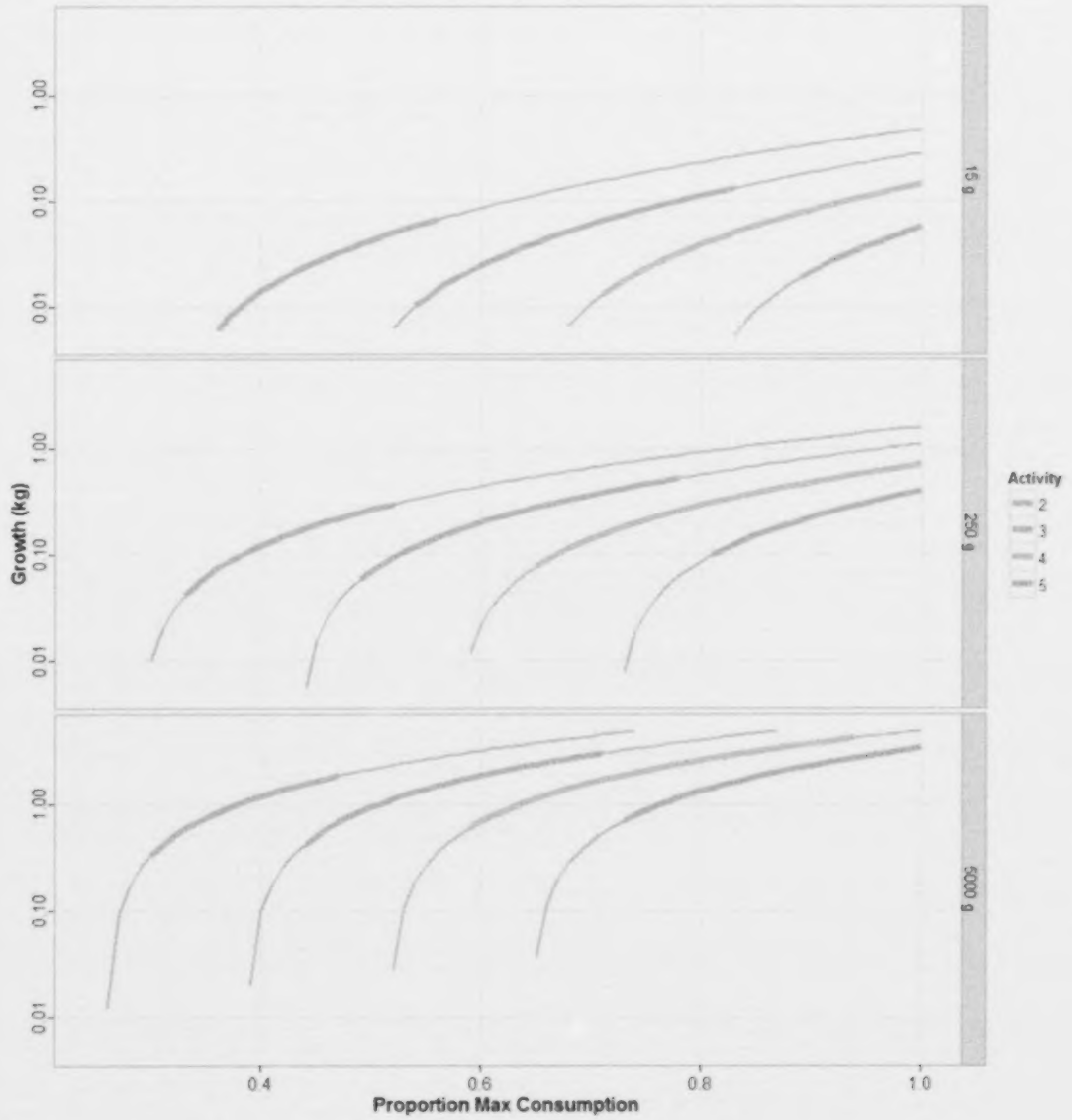

Figure 1.2. Simulation results for annual growth using prey-independent consumption (PIC). The proportion of maximum consumption (x-axis), initial carp weight (right y-axis), and activity levels (different lines) were varied. Growth using PIC is independent of prey energy density. The thick portion of the curves represents the range of expected growth based on an energy budget with 5–20% of consumed energy put towards growth.

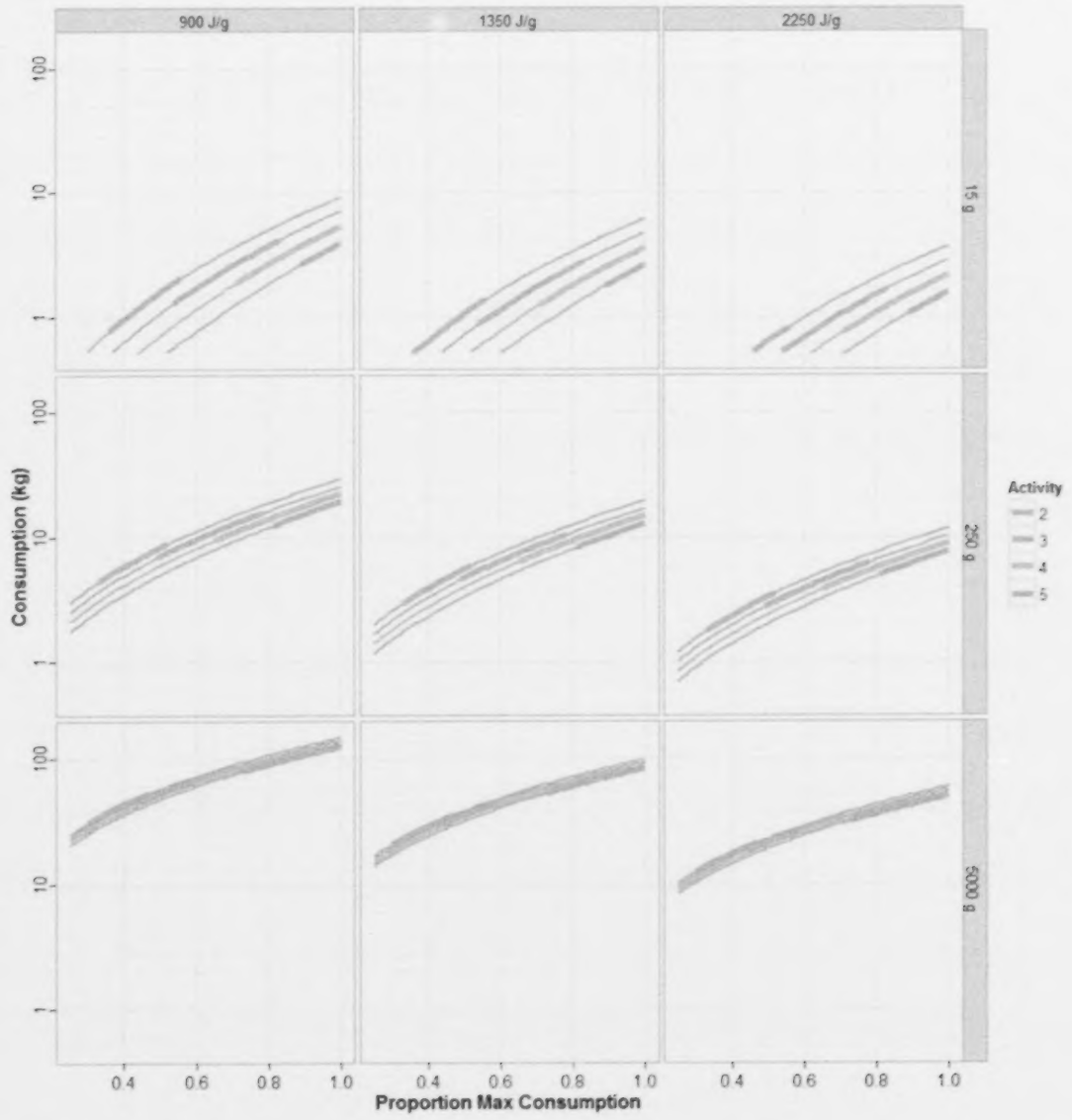

Figure 1.3. Simulation results for annual consumption using prey-independent consumption (PIC). The proportion of maximum consumption (x-axis), initial carp weight (right y-axis), prey energy density (top x-axis) and activity levels (different lines) were varied. The thick portion of the curves represents the range of expected growth based on an energy budget with 5–20% of consumed energy put towards growth.

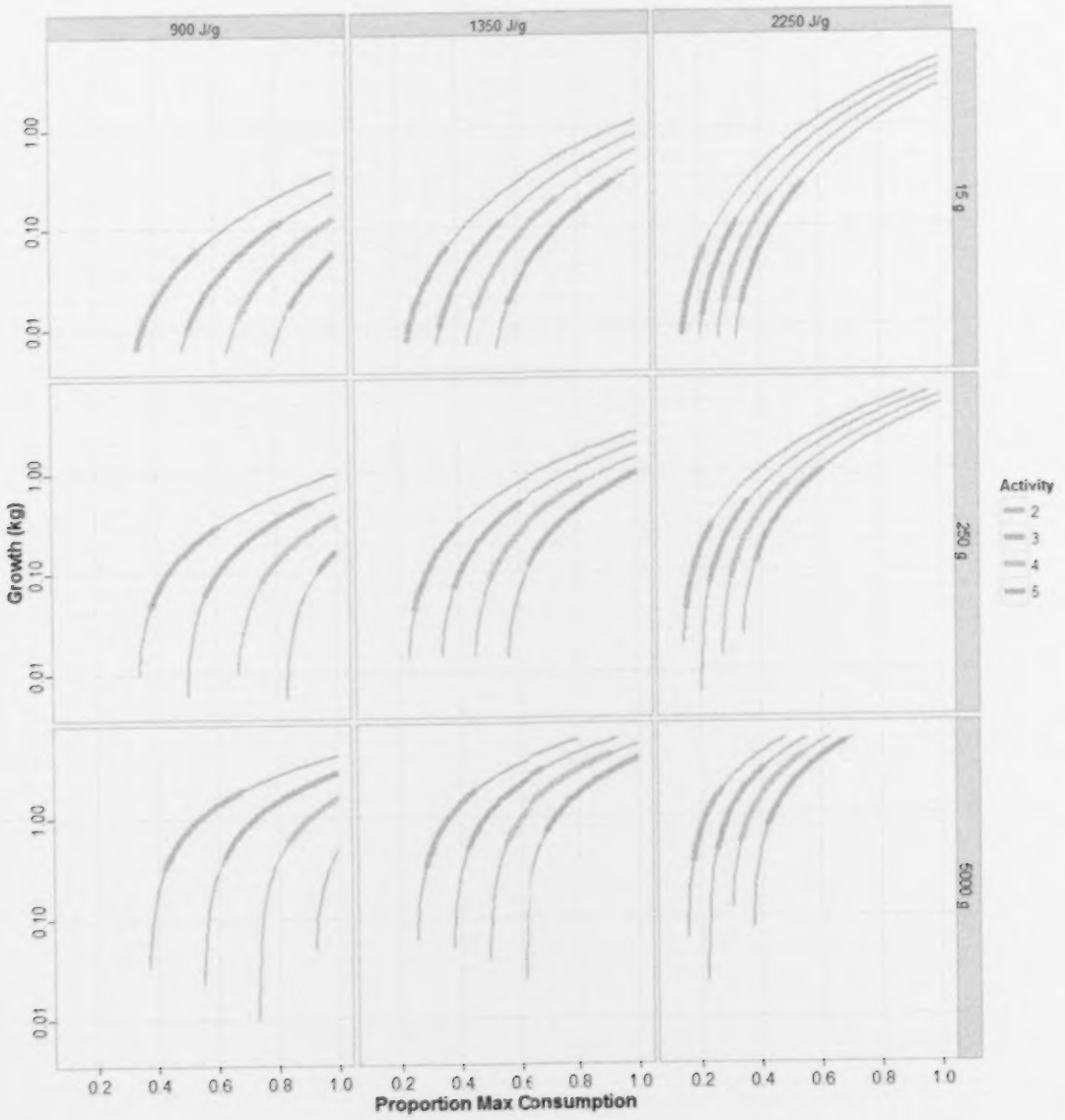

Figure 1.4. Simulation results for annual growth using prey-dependent consumption (PDC). The proportion of maximum consumption (x-axis), initial carp weight (right y-axis), prey energy density (top x-axis) and activity levels (different lines) were varied. The thick portion of the curves represents the range of expected growth based on an energy budget with 5–20% of consumed energy put towards growth.

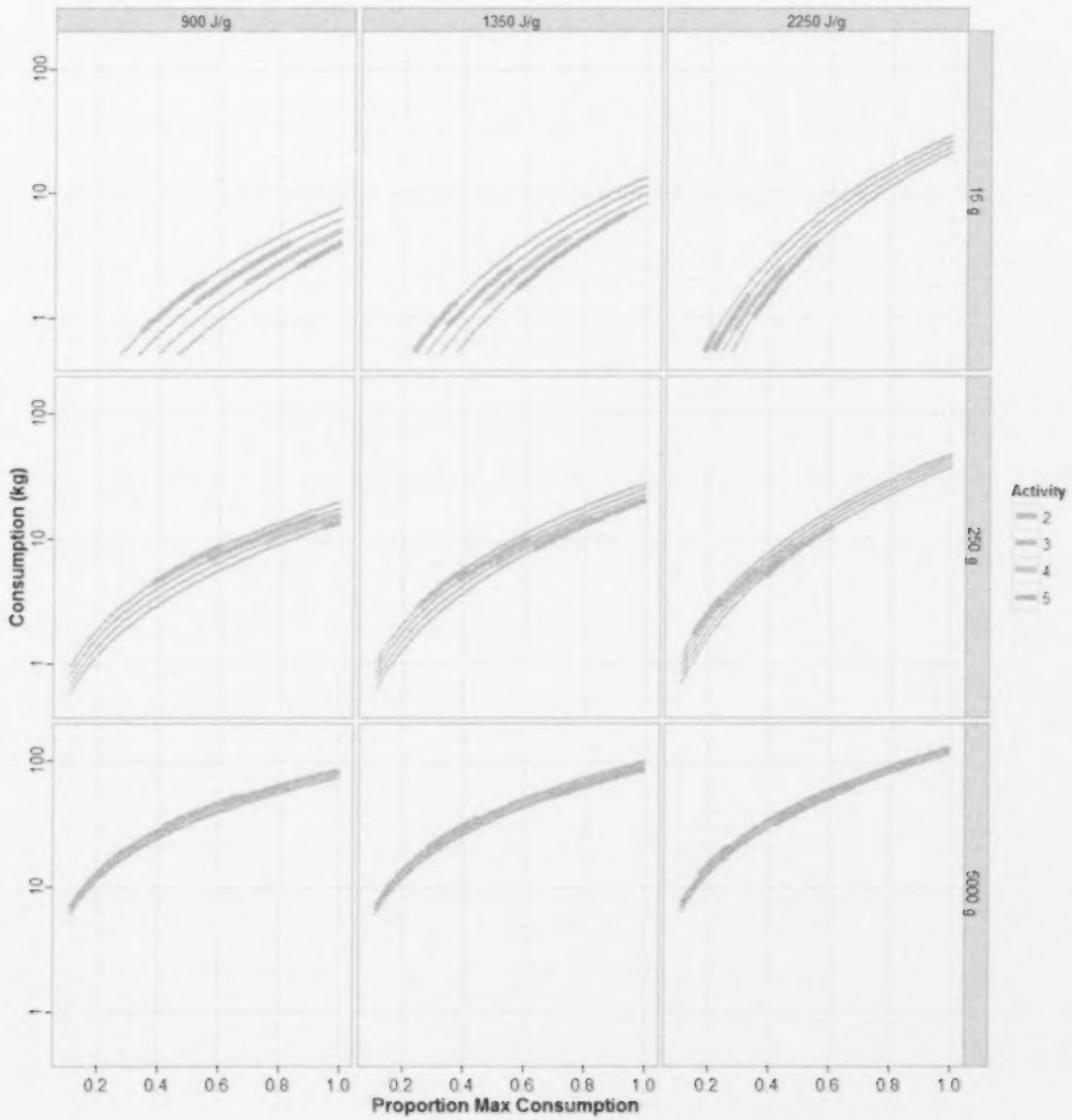

Figure 1.5. Simulation results for annual consumption using prey-dependent consumption (PDC). The proportion of maximum consumption (x-axis), initial carp weight (right y-axis), prey energy density (top x-axis) and activity levels (different lines) were varied. The thick portion of the curves represents the range of expected growth based on an energy budget with 5–20% of consumed energy put towards growth.

Positive growth is achieved for all age classes with p-values less than 1 and with constant activity levels up to 5 times the resting rate (much higher than would be expected under natural conditions). This suggests that within the Great Lakes, and using various diets, Grass Carp will be able to survive and grow to a reproductive size between ages 3–6. When using PIC, growth is independent of prey energy content with the same growth patterns produced regardless of prey source. Using PDC, growth is more rapid and achieved with lower consumption levels as prey energy density increases. Larger fish (5 kg), using a low energy prey source (900 J g^{-1}), and a high activity level (5) were not able to achieve at least 5% somatic growth (Figure 1.5 bottom left panel). This represents a relatively extreme case and was the only instance where positive growth was not possible.

Consumption is dependent on prey energy density using both consumption equation forms, with consumption decreasing as energy density increases; however, using PDC there is the potential for greater annual growth and therefore greater consumption as energy density increases. In general, annual consumption levels are high. For example, a 5 kg (4-year old) fish with a 1350 J g^{-1} diet (assuming PIC), and an activity level of 2–3 would consume between approximately 20 and 65 kg of plant matter annually, with an expected annual somatic growth of 0.3 to 3 kg (representing 5–20% of its annual energy budget).

We present (Figure 1.6) an example of a possible growth pattern and the resultant amount of consumption based on specific assumptions about fish activity and reproductive behaviour which may differ in reality. We were able to replicate this growth pattern predicted by a von Bertalanffy growth curve using each of the possible parameter combinations that satisfied our parameterization criteria (Figure 1.5, bottom panel); however, this required large p-values for age 1 fish (0.71–0.89). The required p-value decreased with age to 0.51–0.59 for an age-15 fish.

Consumption was high with a minimum of over 50 kg $year^{-1}$ by age-5 and up to almost 90 kg $year^{-1}$ by age-10. The cumulative consumption ranged between approximately 800 and 1100 kg of ingested plant matter by age-16. The minimum required annual consumption (Figure 1.6, top right panel, red squares), which we defined as the amount of food necessary to maintain weight with no spawning effort, was as low as 3.4 kg for age 1 (290 g) fish but up to 53.8 kg for an age-15 fish based on the mean parameter combinations for PIC and PDC. Weight maintenance required p-values around 0.3. These consumption values approximate the minimum requirements for winter survival.

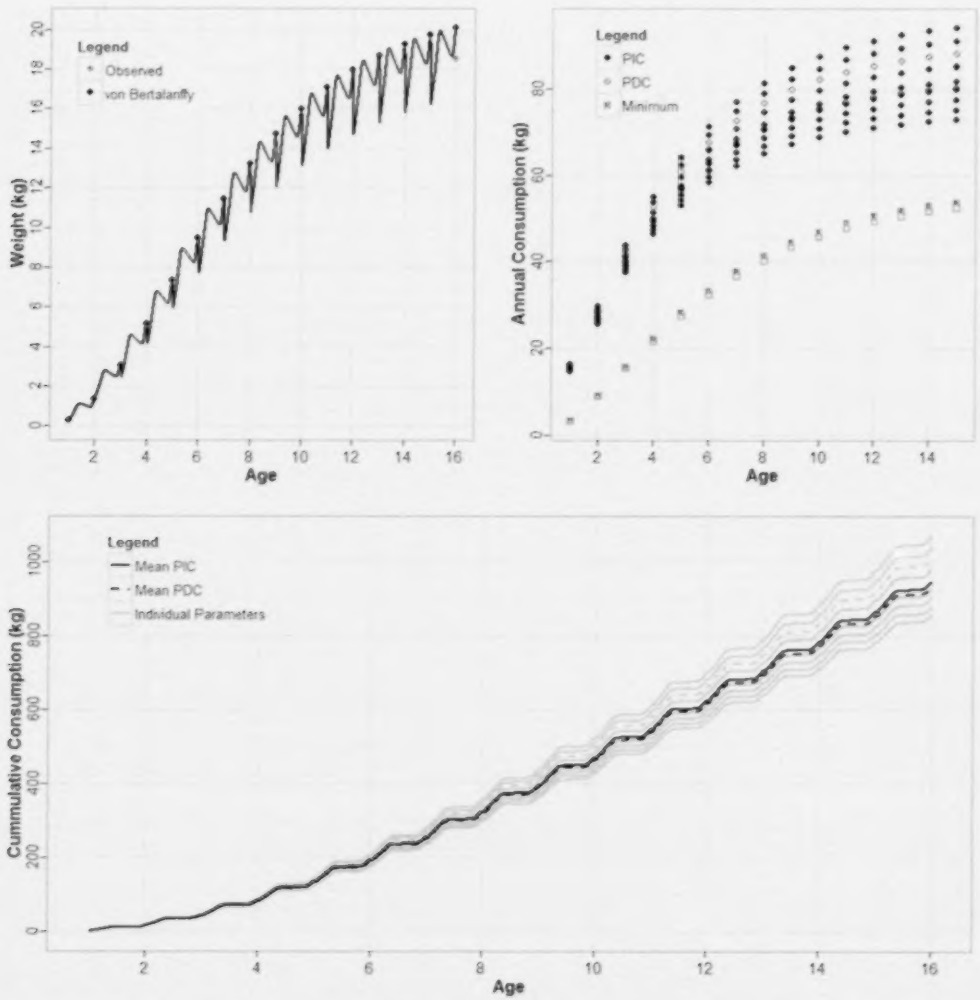

Figure 1.6. Simulated growth and consumption for Grass Carp. Top left: Grass Carp growth matched to a von Bertalanffy growth function (VBGF) and observed triploid Grass Carp from the Grand River in 2013 (red points). The growth pattern is the same for prey-independent (PIC) and prey-dependent (PDC) consumption. Top right: Total annual consumption using the individual parameter combinations for PIC and PDC to display the possible range of annual consumption values and the minimum annual consumption required to maintain initial weight (at age) using the mean relationships for PIC (closed square) and PDC (open square). Bottom: Cumulative consumption needed for VBGF growth using the mean relationships for PIC and PDC (black lines). To display the range of possible cumulative consumption values each of the individual parameter combination (grey lines) is plotted as well.

Model sensitivity

The most sensitive parameters (Table 1.2) were similar when using the different consumption forms (PIC and PDC); however, PDC tended to generate higher sensitivities for growth. Growth was highly sensitive to the allometric exponents in the consumption and respiration equations and approximately linearly sensitive to the consumption intercept and the egestion parameter. Total consumption was primarily sensitive to the respiration exponent and the egestion parameter.

Table 1.2. Sensitivity analysis of growth (final weight) and consumption for a 2 year old Grass Carp consuming a prey item with an energy density of 1350 J g^{-1} and an activity level of 2.5 over one year. Sensitivity was calculated using both prey-independent (PIC) and prey-dependent (PDC) consumption.

Consumption

		Growth		Consumption	
Parameter	Consumption	–10%	+10%	–10%	+10%
a_c	PIC	–10.18	10.96	0	0
	PDC	–10.56	11.31	0	0
b_c	PIC	29.21	–19.24	–0.087	0.087
	PDC	40.62	–24.17	–0.11	0.11
te_1	PIC	3.46	–3.26	–0.38	0.39
	PDC	3.63	–3.41	–0.37	0.38
te_2	PIC	3.42	–3.48	–0.28	0.25
	PDC	3.57	–3.62	–0.27	0.25
te_3	PIC	–0.21	–0.018	–0.022	0
	PDC	–0.21	0.0017	–0.021	0
te_4	PIC	0.0016	–0.019	0	0
	PDC	0.0017	–0.019	0	–0.002

Respiration

		Growth		Consumption	
Parameter	Consumption	–10%	+10%	–10%	+10%
a_R	PIC	7.28	–6.96	–4.79	4.81
	PDC	6.54	–6.27	–4.75	4.77
b_R	PIC	–18.66	16.76	14.47	–10.94
	PDC	–17.26	15.27	14.50	–10.94
c_R	PIC	4.76	–5.03	–2.84	3.08
	PDC	4.23	–4.49	–2.83	3.06
a_S	PIC	0.87	–0.86	–0.81	0.83
	PDC	0.90	–0.89	–0.81	0.83

Waste

		Growth		Consumption	
Parameter	Consumption	–10%	+10%	–10%	+10%
a_F	PIC	10.97	–10.19	–9.09	11.11
	PDC	11.31	–10.56	–9.09	11.11
a_U	PIC	0.94	–0.94	–0.88	0.90
	PDC	0.98	–0.97	–0.88	0.90

DISCUSSION

We created a bioenergetics model for Grass Carp to address a number of questions pertaining to the potential invasion of the Great Lakes. The first question we posed was whether YOY Grass Carp would be able to exhibit positive growth sufficient to survive the first winter? Based on the simulation conditions, it appears that YOY Grass Carp will be able to exhibit positive growth that is sufficient to survive the first winter (Figure 1.2 and 1.4, top row). These simulations assume a diet of entirely aquatic plants while in reality YOY may supplement plant material with animal sources, at least during the first month of life (Cudmore and Mandrak

2004). Because animal food sources tend to have higher energy density, incorporating these prey would increase the likelihood of positive first year growth in the Great Lakes, which our simulations suggest can be achieved even at high activity levels and a diet of low energy density food. Ultimately, the growth rate potential for Grass Carp will be dictated by energetic quality, density, and spatial patchiness of the prey.

Our second question asked how well will Grass Carp grow/survive if they feed exclusively on *Cladophora* spp.? *Cladophora* is a filamentous alga that is abundant in the Great Lakes (Auer et al. 2010) and has reached nuisance levels in Lakes Erie and Ontario (Depew et al. 2011). Grass Carp have previously shown a preference for *Cladophora* (Pípalová 2002) so there is the potential that *Cladophora* will represent a significant prey source for invading Grass Carp. We represent *Cladophora* as having an energy density of approximately 1350 J g^{-1} (Paine and Vadas 1969, Roth et al. 2006) but it may be as low as 1000 J g^{-1} (Carefoot 1973, Gray and Ward 1979). Grass Carp were able to survive and grow when feeding on prey with an energy density of only 900 J g^{-1} even with high activity costs. Higgins et al. (2005) measured the areal coverage and biomass of *Cladophora* at 24 near shore sites (<5 m in depth) along the northern shoreline of Lake Erie's eastern basin between 1995 and 2002. Median areal coverage was 94% with a median biomass of 171 g m^{-2} dry weight (Higgins et al. 2005). Assuming *Cladophora* are 85% water (Carefoot 1973) then a single 5 kg Grass Carp could grow up to 3 kg by consuming the *Cladophora* produced in approximately 70 m^2 (with an activity level of 3 and a food energy density of 1350 J g^{-1}). This however does not take into account any loss in production from early season grazing.

The third question we posed asked what is the consumptive pressure exerted by Grass Carp of different sizes/stages on aquatic vegetation? To address the lifetime impacts of Grass Carp we estimated the required amount of consumption of aquatic plants to replicate a von Bertalanffy growth curve. Cumulative consumption of macrophytes through age-15 ranged from over 800 to almost 1100 kg. Annual consumption was over 50 kg by age-5 and up to 90 kg by age-10. Therefore, consumption of aquatic vegetation by Grass Carp in the Great Lakes is expected to be high (though actual values may differ from these reported estimates) and Grass Carp represent a new and significant threat to macrophyte biomass.

Macrophyte consumption is not a common feeding strategy among freshwater fish species and in freshwater environments algae are typically grazed more intensely than macrophytes (Cyr and Pace 1993). There are few herbivorous species native to the Great Lakes. Gizzard Shad (*Dorosoma cepedianum*) can maintain an entirely herbivorous diet as an adult, though with alga as a primary food source (Scott and Crossman 1973). Some invasive generalists such as, Common Carp (*Cyprinus carpio*), Goldfish (*Carassius auratus*), and Rudd (*Scardinius erythrophthalmus*) may use macrophytes as a substantial portion of their diet.

Rudd, an invasive cyprinid, has maintained an abundant population in Lake Erie (Kapuscinski et al. 2012). Rudd is omnivorous with plant matter on average making up 67% of its diet and has displayed a selectivity for macrophyte species similar to Grass Carp (Kapuscinski et al. 2014). Plant consumption of Rudd during the summer was measured in a eutrophic lake in Finland (Nurminen et al. 2003) for multiple age classes. Consumption generally increased with age and peaked in the late summer similar to our projections for Grass Carp. Relative to Grass Carp plant consumption was very low peaking for age-6 Rudd (approximately 60 g in weight) at 143 g_{prey} $fish^{-1}$ over 90 days (Nurminen et al. 2003). Based on these results, total plant consumption by Rudd over its lifetime would be less than that of Grass Carp during its first year of life (Figure 1.2 and 1.4, top row).

Consumption of macrophytes by Grass Carp in the Great Lakes may be greater than other taxa such as, crayfish, snails and waterfowl (Lodge 1991). Aquatic macrophytes in Lake Erie provide

food for several species of migrating waterfowl (Knapton and Petrie 1999). It is unclear what the extent of waterfowl grazing on macrophytes is in the Great lakes. At Long Point, Lake Erie, in 1998 and 1999 above ground macrophyte biomass averaged approximately 180 g m^{-2} dry weight in late summer (Badzinski et al. 2006). This was reduced by 80% by late fall due to the combined effect of consumption by waterfowl (primarily diving and dabbling ducks) and other small aquatic consumers, wave action, and senescence (Badzinski et al. 2006). Grass Carp consumption was greatest in mid- to late-summer, prior to the arrival of migrating waterfowl and therefore could significantly reduce the macrophyte standing crop available to waterfowl. It is evident that Grass Carp will present a considerable threat to Great Lakes' macrophytes and represent a significant competitor to native waterfowl.

The fourth and final question we addressed was how much food is required for an adult Grass Carp to maintain their body mass. Using the same modelling assumptions as for question 3, but with no spawning, we estimated the consumptive requirements to maintain body mass (having an equal weight one year later). The consumption necessary to just maintain body weight for adult Grass Carp was relatively high. A reproductive sized Grass Carp weighing approximately 3 kg required around 15 kg of macrophytes annually to simply maintain their body weight. This is likely achievable based on a mean macrophyte biomass at Long Point, Lake Erie (180 g m^{-2} dry weight; Badzinski et al. 2006) and would require 12.5 m^2 of vegetated habitat (assuming 85% water content for macrophytes).

The amount of food required by other Asian carps, Bighead and Silver carps, was also estimated to be relatively high (Cooke and Hill 2010). This led the researchers to conclude that Bighead and Silver carps will not be able to survive in many open water regions of the Great Lakes. An exception was Lake Erie where both carps were able to express positive growth in the western and central basins. Anderson et al. (2015) also concluded that Bighead and Silver carps will likely be able to survive in Lake Erie. Similarly we expect Grass Carp to be able to express positive growth in the coastal regions of Lake Erie.

The maintenance requirements of Grass Carp were estimated to be lower than that of Silver and Bighead carps. Cooke and Hill (2010) estimated the consumption requirements to maintain body weight for resting 10 g, 70 g, and 2400 g individuals at 20 °C, to be 1.4, 6.1 and 91 kJ d^{-1} for Silver Carp and 1.3, 5.1, and 61 kJ d^{-1} for Bighead Carp. The consumption required by resting Grass Carp (ACT = 1) was only 0.65, 2.36, and 24.4 kJ d^{-1}. An activity level of 3 was required to produce values close to those of Silver and Bighead carps (1.96, 7.09, and 73.3 kJ d^{-1}). The difference among these species likely comes from the respiratory allometries used in the models. The updated bioenergetics model (Anderson et al. 2015) used the same metabolic parameters and therefore the maintenance requirements would remain similar. The allometry used for Grass Carp had both a lower intercept (0.0019) and greater slope (0.3364 or 0.339) compared to the Silver Carp (a_R = 0.0028, b_R = 0.239) and Bighead Carp (a_R = 0.0053, b_R = 0.299). It is possible that this reflects real biological differences among the species but it may also be the result of parameter uncertainty. Anderson et al. (2015) pointed out that the estimates of resting respiration used in the Bighead and Silver carps bioenergetic model were from fish that were not truly resting and likely under stress. We assume that the Grass Carp respiration estimates were from a truly resting fish and represent a minimum metabolic requirement. Therefore it is possible that the 'resting' estimates for Bighead/Silver and Grass carps are not representative of the identical activity levels.

Uncertainties

Few experimental estimates of an allometric consumption relationship for Grass Carp exist. This along with the very high sensitivity for the allometric exponent parameter leads to much uncertainty in the model output. Many anecdotal accounts of high Grass Carp consumption exist

(e.g., Shireman and Maceina 1981, Wattendorf and Anderson 1984) which exceed the highest possible consumption value using either consumption form included in this model. For example Shireman and Maceina (1981) estimated consumption of Grass Carp >6 kg stocked in a Florida pond to be 0.25–0.28 $g_{prey}\ g_{fish}^{-1}\ d^{-1}$. From our model, the maximum consumption for a 6 kg Grass Carp, assuming a prey energy density of 1350 $J\ g^{-1}$, is 0.07 and 0.078 $g_{prey}\ g_{fish}^{-1}\ d^{-1}$ for prey-independent and prey-dependent consumption, respectively. It is possible that consumption rates could be much higher than our model estimates; however, this would need to be offset with more egestion or increased respiratory costs or it would result in unreasonably large Grass Carp. More information on consumption rates is required for more confidence in the growth and resultant consumption values reported in this study.

Estimates of egestion vary widely in the literature ranging from 35% (Cui et al. 1992) to 87% (Fischer 1972). We chose a middle value of 50% which has support in the literature (van Dyke and Sutton 1977, Cui et al. 1994). There remains the potential for greater egestion values in wild populations or egestion related to food availability, body size, or prey type. Total consumption proved sensitive to this parameter in the model results.

Many of the literature values used in parameterizing the model are from small, young Grass Carp. For example, our source for the consumption intercept was based on individuals ranging in size from 15–450 g (Fischer 1973) and the sources for the egestion parameter measured individuals ranging in size from 12–13 g (Cui et al. 1994) and 225 – 491 g (van Dyke and Sutton 1977). We then use these values and extrapolate to individuals up to 20 kg in weight. This introduces a potential bias in the results if rates change with size and age more or less than the model suggests. Fitting the allometric exponents for the respiration and consumption values may reduce some of this bias ensuring that the results are within reasonable bounds; however, more research needs to be done examining consumption, egestion, and other bioenergetics processes for the broader range of carp sizes.

Little information was available related to the spawning behaviour and costs for Grass Carp. We chose a value of 15% of body mass as the spawned biomass which is consistent with other species (Hanson et al. 1997) and some Grass Carp observations (Shireman and Smith 1983). Less information was available describing spawning behaviour. Grass Carp are potamodromous and will migrate up stream at least 50 km (Fedorenko and Fraser 1978). We assume a two week period is required to migrate to the spawning location, spawn, and return and also that no feeding occurs during this period (Fedorenko and Fraser 1978). Total annual spawning cost, based on these assumptions, was around 20% of body weight of which 15% was attributable to gonad development; therefore only the remaining 5% was due to the spawning migration. This means differences between our assumed spawning behaviour and actual events will likely not impact our model results markedly.

Interpretation

The potential for higher consumption rates than we have used suggests that initial impacts of a Grass Carp invasion may be even greater than this model predicts. It is unlikely that that level of consumption could be sustained based on both the prey availability and the consumptive limitations of the individual Grass Carp. There is, however, the potential for a boom bust cycle where high initial consumption rates exhaust the available resources and the relatively high maintenance costs of adult Grass Carp results in high mortality.

The results of this model are more likely representative of a sustained population with more reasonable consumption rates that could be maintained throughout the life of the fish. These results point to a persistent breeding population provided that adequate spawning habitat is available (Kocovsky et al. 2012).

The model consumption estimates only account for the amount of macrophytes actually ingested by the Grass Carp. If Grass Carp have a preference for a certain part of a plant, do not consume it entirely but damage it beyond what is ingested, the impacts will be magnified. Many macrophyte grazers destroy much more macrophyte tissue than they consume (Lodge 1991). This may account for some of the differences in consumption/impact estimates from this model and other observations (e.g., Scott and Orr 1970, Shireman and Smith 1983, Pípalová 2002). If Grass Carp activities result in plant death/damage, the impact will be greater than estimated consumption alone.

CONCLUSION

We presented a Grass Carp bioenergetics models and determined that growth and survival in the Great Lakes is possible using a variety of diets including solely *Cladophora*. The impacts of a sustained breeding population are predicted to be large with adult individuals consuming up to 90 kg of macrophytes annually. These impacts could be amplified if feeding preference or foraging behaviour result in plant damage beyond what is consumed.

2.0 EVALUATING THE NET REPRODUCTIVE VALUE OF GRASS CARP IN THE GREAT LAKES FOR POTENTIAL ESTABLISHMENT

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INTRODUCTION

Grass Carp (*Ctenopharyngodon idella*) has been globally introduced to waterways for purposes of controlling invasive macrophytes, but is also perceived as an invasive species when populations cause unwanted impacts to native macrophytes (Wittmann et al. 2014). Grass Carp were introduced to the United States in 1963 and have since been widely distributed for macrophyte control. However, in the mid 1970s, scientists and managers became concerned about undesirable impacts, such as lowered water quality and localized loss of native macrophytes where high densities of Grass Carp were stocked (Mitchell and Kelly 2006). In 1978, Stanley concluded that Grass Carp could establish in the United States if sufficient numbers of fish escaped from ponds or were stocked in locations with suitable conditions for reproduction to occur. Plagued by increasing escapes and captures of Grass Carp in the wild, the United States Fish and Wildlife Service (USFWS) started the National Triploid Grass Carp Inspection and Certification Program which was tasked with inspecting the production of sterile (triploid) Grass Carp (Piferrer et al. 2009) to mitigate the potential threat posed by potential widespread establishment of Grass Carp.

Grass Carp are currently established throughout the Mississippi River basin of the United States and recent captures of diploid individuals in the Great Lakes basin have raised concerns that a sufficient number of individuals are present to form an established, self-sustaining population (Wittmann et al. 2014). In 2012, juvenile Grass Carp were captured in the Lake Erie basin and otolith microchemistry revealed these fish were likely recruited within the Great Lakes Basin (Chapman et al. 2013). We are now faced with building upon previous risk assessments (Mandrak and Cudmore 2004, Wittmann et al. 2014) to identify the current threat posed by Grass Carp establishment, spread, and impacts to the Great Lakes. A life-history based, Grass Carp population model is absent from previous Grass Carp risk assessments. The development of a population model will help to further inform evaluation of the current establishment risk.

In life-history based population models, the net reproductive rate (R_0) is a common metric for evaluating population dynamics and is defined as the number of female offspring produced by a female in a population. If the net reproductive value is less than one, then the population is not expected to persist. If R_0 is greater than one, then the population is expected to grow. The use of R_0 has until recently been very difficult for matrix models of population growth due to an absence of an analytical solution (Caswell 2002, de-Camino-Beck and Lewis 2008). However, R_0 is advantageous for management considerations because it explicitly connects life cycle structure with demographic parameters. This allows for evaluation of management strategies that interfere with the cycle structure (e.g., removing one or more reproductive stages) or shifting demographic parameters (i.e., reducing fecundity or survival).

Here we use descriptions of Grass Carp life history to form a life history graph, reduce the graph to a representation of the R_0 function, and then parameterize the function. We use the best available estimates reflecting the expected life history of Grass Carp found in similar habitat conditions to those of the Great Lakes. The focal question of this exercise is, "Given the best understanding of the biology of Grass Carp and the potential habitat of the Great Lakes, is there evidence for population growth?" Then, using the R_0 function, we evaluate three management scenarios/questions:

1) How low would adult survival need to be in order to achieve an $R_0 = 1$?,
2) How effective would actions to increase egg mortality, such as through mechanical, chemical, or biological treatment need to be in order to get $R_0 = 1$?, and
3) How would low-density mate finding affect the estimate of $R_0 = 1$?

Finally, the influence of demographic stochasticity on the extinction probability is assessed for small populations of Grass Carp to reveal the probability of establishment.

METHODS

Estimating the net reproductive value

Grass Carp are long-lived fish (10+ years) that become sexually mature at approximately four years of age (Table 2.1). A life history graph (Caswell 2002) of Grass Carp was developed to show the transition between life stages, where Js are juvenile states, A is the adult state, *t*s are transition probabilities (i.e., the likelihood of entering the next age state), *f* is the fecundity of adults resulting in young-of-year (YOY) juveniles (Figure 2.1).

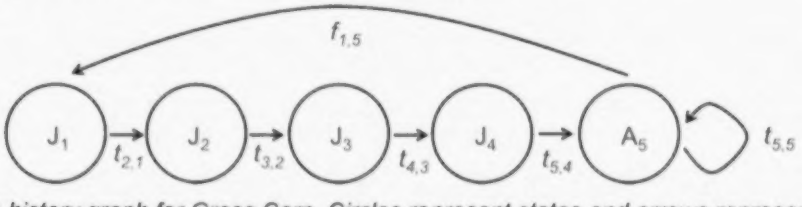

Figure 2.1. Life history graph for Grass Carp. Circles represent states and arrows represent transitions.

Using the graph reduction approach for R_0 (de-Camino-Beck and Lewis 2007, 2008), we find the function of R_0 is,

$$R_0 = f_{1,5}\left(t_{2,1}t_{3,2}t_{4,3}\frac{p_{5,4}}{1-t_{5,5}}\right)$$

Table 2.1. Reported parameter values and sources (from literature search and Bogutskaya et al. (2017)). Full references for all data, except Li (1999) and Rottman (1977), can be found in Bogutskaya et al. (2017).

Description	Value	Type	Location	Citation
Probability of adult survival	0.63	River	Amur River, Russia	Abrosov and Bauer 1955
Probability of adult survival	0.68	Reservoir	North Carolina, USA	Li 1999
Probability of juvenile survival	0.48	Pond	Krasnodarskiy Kkrai, Russia	Bizyayev 1966
Probability of juvenile survival with piscivore fish present	0.0002	Pond	Columbia, Missouri USA	Rottman 1977
Probability of juvenile survival without piscivore fish present	0.0518	Pond	Columbia, Missouri USA	Rottman 1977
Probability of juvenile survival	0.71	Pond	Szarvas, Hungary	Abdule-Amir et al. 1989
Probability of juvenile survival	0.7	Pond	Szarvas, Hungary	Abdule-Amir et al. 1989
Probability of juvenile survival	0.76	Pond	Szarvas, Hungary	Abdule-Amir et al. 1989
Probability of juvenile survival	0.75	Pond	Szarvas, Hungary	Abdule-Amir et al. 1989
Probability of recruitment (egg to juvenile)	0.65	River	Syr Darya River, Uzbekistan	Verigin et al. 1978
Average Fecundity	703,860	Reservoir	Amu Darya River, Turkmenistan and Uzbekistan	Abdullayev and Khakberdiyev 1980
Average Fecundity	756,000	River	Terek River	Abdusamodov 1986
Average Fecundity	945,000	River	Terek River	Abdusamodov 1986
Average Fecundity	820,000	River	Amur River, Russia	Gorbach 1972
Average Fecundity	635,000	River & Reservoir	Kapchagay Reservoir & Amur River, Russia	Karpov et al. 1989
Average Fecundity	800,000	Reservoir	Kapchagay Reservoir	Mitrofanov et al. 1992
Average Fecundity	820,000	River	Amur River, Russia	Mitrofanov et al. 1992
Probability of being female	0.4	River	Ili River	Faryshev and Bashunov 1980

Description	Value	Type	Location	Citation
Probability of being female	0.5	Reservoir	Reservoir on the Ili River	Karpov et al. 1989
Probability of being female	0.52	Reservoir	Kapchagay Reservoir	Karpov et al. 1989
Probability of being female	0.3	River	Syr Darya River, Uzbekistan	Miroshnichenko and Kamenetskaya 1978
Age at maturity	M: 7 F: 5	Reservoir	Amu Darya River, Turkmenistan and Uzbekistan	Abdullayev and Khakberdiyev 1980
Age at maturity	M: 4 F: 5	River	Terek River	Abdusamodov 1986
Age at maturity	M: 7 F: 7	River	Amur River	Gorbach and Kryktin 1981
Age at maturity	M: 3 F: 4	Lake	Balkhash Lake	Karpov et al. 1989
Age at maturity	F: 3	River	Amur River	Makeyeva 1968
Age at maturity	F: 4	River	Yangtze River	Makeyeva 1968
Max No. of female spawning efforts	3			Gorbach 1965

Parameter values

Grass Carp parameter values were obtained from the primary literature using ProQuest, ISI Web of Science, and Scopus with keyword search terms "Ctenopharyngodon idell*" or "Grass Carp", along with one of three sets of terms:

1) "survival" or "mortality", or "tolerance", or "longevity" or "viability";
2) "fecundity", or " brood stocks", or "eggs", or "sexual maturity", or "recruitment", or "reproduction"; and
3) "probability, or "ratio", or "odds" or "proportion", and "female", or "gender", or "sex".

Studies were retained if they included a measure of survival, sex ratio, or fecundity for Grass Carp under natural or unassisted conditions (e.g., wild or naturalized populations). Studies of Grass Carp in controlled experiments in cages, aquaria, or stocked ponds were excluded.

In addition, Russian language peer-reviewed journal sources, books, government publications and additional literature were reviewed and translated individually into an annotated bibliography that summarizes key findings and conclusions from research conducted on Grass Carp (Bogutskaya et al. 2017). This annotated bibliography was also searched for the above listed parameters (survival, sex ratio and fecundity). Table 2.1 provides details of the parameters found from the literature search.

YOY juveniles are the most susceptible to predation. In a manipulated system with juvenile Grass Carp and piscivorous fish, Rottmann (1977) found that survival probability was small, $t_{2,1} = 0.0002$. In contrast, the transitions through J_2 to J_4 juvenile states on to adulthood ($t_{3,2}$, $t_{4,3}$, and $t_{5,4}$) appear to have similar survival probabilities, 0.594 (± 0.304) and are highly susceptible to common angling practices (D. Chapman, U.S. Geological Survey (USGS), pers. comm.). Adult survival is expected to be high because these large fish have few predators, $t_{5,5} = 0.63$ (± 0.035). The average number of eggs per female Grass Carp is 782,837 (± 98,461) with a fixed estimate of 65% of eggs being recruited to juveniles (Bogutskaya et al. 2017) and probability of being female of 0.43 (± 0.1). Table 2.2 provides details of the parameters used in this study.

Table 2.2. Average parameter estimates used for the model.

Parameter	Mean (Std. Dev.)	n
Probability Adult Survival	0.63 (0.035)	2
Probability Juvenile Survival (YOY)	0.0002 (no error)	1
Probability Juvenile Survival	0.594 (0.304)	6
Average Fecundity	782,837 (98,461)	7
Probability of Being Female	0.43 (0.1)	4
Number of female spawning events	3 (no error)	1

Age of reproductive maturity

For this work, female Grass Carp were assumed to be reproductively mature at age class four. However, some observations have identified age of maturity to occur as early as two and as late as seven or eight (Table 2.1). The R_0 equation can be modified and solved for various lengths of reproductive maturity assuming that shortening or lengthening the maturity only changes the number of transitions between juvenile age and adulthood and has approximately the same parameter estimates (Table 2.3).

Table 2.3. R_0 functions for variation in female reproductive maturity of Grass Carp. Equation for maturity at 4 years of age provided above.

Description	R_0
Mature at 2 years	$f_{1,3}\left(\frac{t_{2,1}t_{3,2}}{1-t_{3,3}}\right)$
Mature at 3 years	$f_{1,4}\left(\frac{t_{2,1}t_{3,2}t_{4,3}}{1-t_{4,4}}\right)$
Mature at 4 years	$f_{1,5}\left(\frac{t_{2,1}t_{3,2}t_{4,3}t_{5,4}}{1-t_{5,5}}\right)$
Mature at 5 years	$f_{1,6}\left(\frac{t_{2,1}t_{3,2}t_{4,3}t_{5,4}t_{6,5}}{1-t_{6,6}}\right)$
Mature at 6 years	$f_{1,7}\left(\frac{t_{2,1}t_{3,2}t_{4,3}t_{5,4}t_{6,5}t_{7,6}}{1-t_{7,7}}\right)$
Mature at 7 years	$f_{1,8}\left(\frac{t_{2,1}t_{3,2}t_{4,3}t_{5,4}t_{6,5}t_{7,6}t_{8,7}}{1-t_{8,8}}\right)$
Mature at 8 years	$f_{1,9}\left(\frac{t_{2,1}t_{3,2}t_{4,3}t_{5,4}t_{6,5}t_{7,6}t_{8,7}t_{9,8}}{1-t_{9,9}}\right)$

Management Scenarios

Scenario/Question 1: Removal of adults

One strategy is to reduce the survival of adult Grass Carp populations. Adult survival for fish matured at four years is the value $t_{5,5}$. If $t_{5,5}$ approaches 1 (i.e., nearly no adult mortality), the value of R_0 goes to infinity representing a population boom. However, if the value of $t_{5,5}$ goes to near zero, and all grass carp essentially become semelparous (i.e., transition to adults, spawn, and die), the value of R_0 reduces to $f_{1,5}\, t_{2,1}\, t_{3,2}\, t_{4,3}\, t_{5,4}$. For any given set of parameters, if $f_{1,5}\, t_{2,1}\, t_{3,2}\, t_{4,3}\, t_{5,4} > 1$, then the population cannot be controlled by harvesting adults, unless adults are harvested before they can spawn.

Scenario/Question 2: Increased egg and juvenile fish predation

Similar to adult survival, there is a critical value of the fecundity (number of surviving female eggs that enter the J_1 stage as YOY) that results in $R_0 = 1$. Removing these eggs, fry, and juveniles would require management actions such as increasing predators in the Great Lakes, chemical treatment of rivers and streams thought to have reproducing Grass Carp, or mechanical treatments of these rivers, such as egg removal from streams (Keller 2014). The critical value for fecundity is therefore,

$$f_{1,5}^{*} = \frac{1-t_{5,5}}{t_{2,1}t_{3,2}t_{4,3}t_{5,4}}$$

If the resulting critical fecundity ($f_{1,5}^{*}$) is very large, then management actions that have even minimal impacts on egg survival would potentially provide an avenue for invasive species management. However, if the critical fecundity is small then nearly all eggs would have to be removed from all streams to induce a declining population.

Scenario/Question 3: Mate finding at low density

Grass Carp introductions into the Great Lakes are possibly widespread over a large geographic and temporal extent. Since the 1990s, there have been small numbers of both triploid and diploid individuals observed across the Great Lakes Basin. While it is unknown where these fish originated from, they were likely the result of multiple introduction events such as escapes of individuals from connected waterways, and potentially from stocks of triploid fish that were contaminated with diploid individuals. As such, diploids may have a difficult time finding each other and mating. Additionally, female Grass Carp may have repeated incremental spawning. We explore the consequence of repeated incremental spawning on population establishment by evaluating R_0 with a modified fecundity term based on chance mating over repeated incremental spawning events. Assuming an equally proportional egg release per spawning event, the random variable of surviving, female eggs is,

$$\Pr(X = x) = \frac{f_{1,5}}{n}\binom{n}{x} p^x (1-p)^{n-x}$$

where n is the number of spawning events, p is the probability of finding a mate at any given event, and the resulting x describes the realized fecundity. The probability of finding a mate, p, is likely dependent on a number of key factors including landscape, potential triploid mating interference, and diploid population density. Unfortunately, there is no information available to make such inferences and we treat p as a free parameter assumed to be small ($p < 0.05$), otherwise, when p is large, the resulting R_0 would default to the original formulation. See Appendix 1 on Distribution of Grass Carp into suitable streams for a more detailed discussion on the threat posed to the Great Lakes by chance aggregation of reproductively viable Grass Carp.

Matrix population modeling

The life history graph (Figure 2.1) can be written as a matrix model A,

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & f_{1,5} \\ t_{2,1} & 0 & 0 & 0 & 0 \\ 0 & t_{3,2} & 0 & 0 & 0 \\ 0 & 0 & t_{4,3} & 0 & 0 \\ 0 & 0 & 0 & t_{5,4} & t_{5,5} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 0 & 218{,}803 \\ 0.0002 & 0 & 0 & 0 & 0 \\ 0 & 0.594 & 0 & 0 & 0 \\ 0 & 0 & 0.594 & 0 & 0 \\ 0 & 0 & 0 & 0.594 & 0.63 \end{bmatrix}.$$

The dominant eigenvalue is the population growth rate, λ. A stochastic population model can be created by letting ts be binomial random variables with $n_{i,t}$ the observed population in stage i at time t, and probability of survival $t_{i+1,i}$. Fecundity can be treated as a Poisson random variable with mean $f_{1,5}$. This model only captures demographic stochasticity - the chance survival and reproduction of individuals from an initial population.

We consider five cases for stochastic model evaluation:

1) Probability of population survival after 20 years for an initial introduction of juveniles to stage (J_1),
2) Probability of survival after 20 years for an initial introduction of juveniles to stage (J_2),
3) Probability of survival after 20 years for an initial introduction of juveniles to stage (J_3),

4) Probability of survival after 20 years for an initial introduction of juveniles to stage (J_4), and

5) Probability of survival after 20 years for an initial introduction of adults to stage (A_5).

The 20-year time horizon is used to allow for full generation time of Grass Carp since this species is long lived (>10 years). Since this model is meant to evaluate only the consequences of demographic stochasticity only, it will likely have high establishment probabilities for adult Asian carp introductions.

RESULTS

Estimating the net reproductive value

Point estimate evaluation of R_0.

Using our best available point estimates, the value of R_0 is 24.8. Being greater than one, we expect Grass Carp to establish populations in the Great Lakes. The interpretation of R_0 is the number of female offspring produced per female offspring. As such, we expect on average 24.8 female offspring to be recruited into the Grass Carp population over the lifetime of a female Grass Carp.

Uncertainty in R_0.

For some parameter estimates we have estimated standard deviations. Using a normal random number generator we account for our uncertainty in parameter estimates resulting in a distribution of R_0. With 1,000 simulations, we observed maximum, median, and minimum R_0 of 515.4, 24.9, and ~0, respectively. With one extreme being ~0 female Grass Carp produced per female over a lifetime, the population would not be able to reproduce enough to replace itself and decline. In contrast, the other extreme, over 500 females recruited to the population would imply rapid recruitment and fast population growth. Approximately 9.3% of observations are less than one. Consequently, we are approximately 90.7% certain that Grass Carp, if introduced into the Great Lakes, will become established based on life history.

If we consider the variability around the parameter estimates as an indication of the likely environmental variability Grass Carp would experience in the Great Lakes, then it is possible that some locations may not be suitable to foster population growth and spread. There is no information available to build a more refined, spatially-explicit connection between survival and fecundity to the estimate of R_0.

Age of reproductive maturity

The consequence of having Grass Carp in the Great Lakes that become reproductively mature earlier (J_2 or J_3) is that R_0 becomes larger. Similarly, longer times to reproductive maturity (J_5 to J_8) maintain R_0 values larger than one (Figure 2.2A). Even with lags in female Grass Carp reproductive maturity, the Great Lakes are still at risk for establishment (Figure 2.2B).

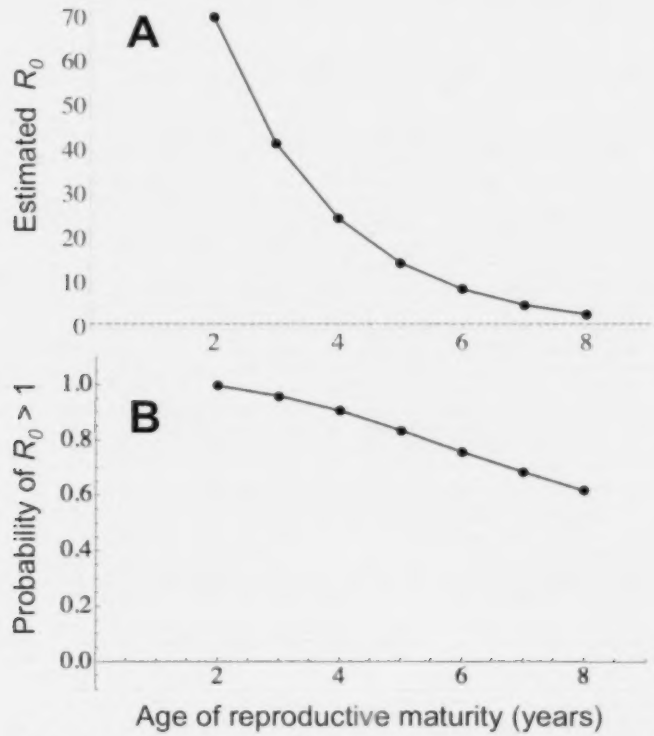

Figure 2.2. R_0 *for variable times of reproductive maturity (A) and the probability of* $R_0 > 1$ *for variable times of reproductive maturity (B). The grey dashed line indicates* $R_0 = 1$. *Regardless of the timing of reproductive maturity for females in the Great Lakes, Grass Carp populations are expected to establish.*

Management scenarios

Scenario/Question 1: Removal of adults

Removing adults is not likely to be a viable strategy for managing Grass Carp. If we take the case where adults are essentially treated as being semelparous, then $R_0 = 9.17$. This implies management of Grass Carp must occur at egg or juvenile fish stages, unless all adults can be harvested before spawning.

Scenario/Question 2: Increased egg and juvenile fish predation (removing eggs)

The fecundity of the average adult female is:

eggs * survival * probability of being female; 782,837 * 0.65 * 0.43 = 218,803. The critical value of fecundity to reduce R_0 to one is 8,827. This represents reducing the egg survival from 0.65 to 0.026. This would imply that every year, the egg survival would need to be reduced to 2.6% in order to cause a population decline.

Scenario/Question 3: Mate finding at low density.

The expected R_0 is invariant to the number of incremental spawning events, $E[x] = n\ p\ f_{1,5}\ n^{-1} = p\ f_{1,5}$ and consequently is dependent only on p, the probability of finding a mate. In low density populations, or if triploids do interfere with fertilization of viable eggs, then we would expect R_0 to be lower until full reproductive potential could be reached. The mate finding probability would

be the same threshold as the effort needed to reduce R_0 egg survival, 0.026. This would imply that for every female there would have to be a 2.6% chance of finding a mate.

Matrix population model

The population growth rate (λ) is 1.7. As reflected previously with R_0, the population is expected to establish and grow. However, using a model of demographic stochasticity, we see that one-time introduction efforts of juvenile Grass Carp of less than 1,000 individuals have only a 0.04% chance of being established after 20 years. Figure 2.3A details the probability of establishment as a function of juvenile introduction effort (number of fish introduced in a specified age class). Demographic stochasticity does very little to buffer against establishment of age classes J_2 to A_5, with high probabilities of establishment with even 10s of individuals introduced (Figure 2.3B).

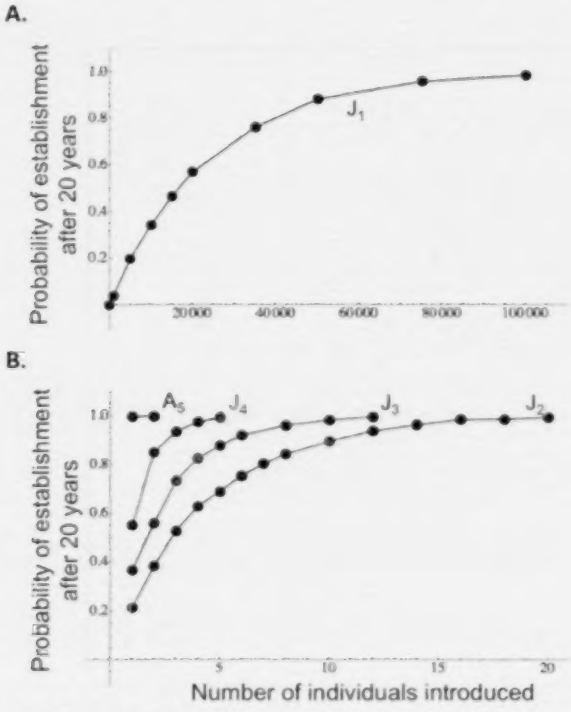

Figure 2.3. Probability of establishment after 20 years for J_1 stage (A) and the remaining J_2 to A_5 (B) age classes. Because the transition probability for J_1 to J_2 is so small, it would take many thousand individuals introduced to likely cause population establishment. In contrast, only 10s of individuals of J_2 to A_5 could be introduced to create an establishment event. This relationship is driven by demographic stochasticity and does not account for reduced survival or fecundity due to environmental stochasticity.

DISCUSSION

Using point estimates, the net reproductive rate (R_0) for Grass Carp in the Great Lakes was estimated to be 24.8, indicating that with our best available information, Grass Carp are likely to establish in the Great Lakes. There was uncertainty in life history estimates, but even with uncertainty considered, over 90% of the estimates had $R_0 > 1$. This indicates that under some environmental conditions that may directly influence survival or reproduction, some introductions efforts may fail, but evidence from the literature indicates that Grass Carp are likely to become established if introduced to the Great Lakes (Chapman et al. 2013, Wittmann et al. 2014). If it is

assumed that uncertainty in the survival and fecundity estimates of Grass Carp life history reflects a diversity of environmental conditions (environmental variability) in the Great Lakes, then it is possible some locations will not support Grass Carp establishment - as indicated by 9.3% of $R_0 < 1$.

As the timing of reproductive maturity for female Grass Carp is also uncertain, R_0 for various life histories was assessed (Table 2.3). The result was that if female Grass Carp became reproductively mature before age 4, then the expected value of R_0 increased to as much as 70 for maturity at age 2 (J_2). The expected R_0 decreased if reproductive maturity was delayed, but never dropped below the critical threshold of $R_0 = 1$. Since there were no records of female Grass Carp becoming reproductively viable after 7 years, we conclude that even if females in the Great Lakes are slow to reach reproductive maturity, it will not impact their ability to become established.

Three management scenarios were considered with the R_0 formulation. The first, removing adults, appears to be very difficult unless a highly effective method for detection and capture of adult Grass Carp before spawning can be developed. Currently, adult survival is estimated to be around 63%. R_0 evaluation indicates that all of the adult population would need to be removed *yearly and before spawning* in order to collapse an established Grass Carp population.

The second scenario, removal of eggs, would likely require excessive effort with potential for minimal results. Egg survival would have to drop from 0.65 to 0.02.

The third scenario is tenuous because of the considerable uncertainty in mate finding behaviour of Grass Carp. Mate finding would necessarily have a very low probability of occurring, 0.026, in order to bring $R_0 = 1$. The number of incremental spawning events does not influence the establishment risk in the mathematical formulation. It should be noted that if Grass Carp have some ability to aggregate, such as pheromone release for mate finding, then there would be virtually no Allee affecting dynamics. For multiple introduction efforts over a wide geographical expanse, it may be reasonable to believe there is a low probability of finding a viable mate, but because of the largely unknown introduction effort of diploid Grass Carp in the Great Lakes and the uncertainty in Grass Carp reproductive behaviour, any potential management suggestions arising from this last scenario would be purely speculative.

While the R_0 approach is relatively new, calculating the population growth rate (λ) using the first dominant eigenvalue of a population matrix is well established (Caswell 2002). In the case of Grass Carp, we find R_0 and λ provide consistent population conclusions that there is evidence that an introduction of Grass Carp will lead to population growth and establishment. While we were able to evaluate R_0 for possible influences of environmental stochasticity, one disadvantage to the R_0 is that it does not account for demographic stochasticity. Using a stochastic population model, we found that demographic stochasticity only has substantial influence on the probability of establishment from an introduction of YOY Grass Carp (J_1; Figure 2.3A). In contrast, only 10s of individuals of J_2 to A_5 stages are needed to overcome demographic stochasticity and establish a population (Figure 2.3B). While these results are consistent with other formulations of Asian carp population dynamics (Cuddington et al. 2014), stochastic matrix models do not consider the possible influence of Allee effects in light of environmental stochasticity (Dennis 2002) and inferences about minimal population size necessary for establishment should be made with caution until better understanding of Grass Carp mating behaviour is known.

3.0 SIMULATION OF OVERWINTER SURVIVAL OF FIRST-YEAR GRASS CARP *CTENOPHARYNGODON IDELLA* IN THE GREAT LAKES BASIN

Lisa A. Jones, D. Andrew R. Drake, and Nicholas E. Mandrak

ABSTRACT

To determine whether Grass Carp (*Ctenopharyngodon idella*) will survive in the Great Lakes basin as a function of temperature, we developed a statistical model to better understand the overwinter survival for young-of-year (YOY) individuals. The model was based on biological attributes derived from primary literature (temperature-driven spawn cues, hatch lengths, and daily growth increments) and daily water temperature regimes specific to nearshore and tributary areas throughout the Great Lakes. A general latitudinal gradient of spawning timing occurred as a function of temperature, with southern regions like the Portage-Burns Waterway in Lake Michigan, the Vermillion River in Lake Erie, and the Genesee River in Lake Ontario exhibiting the earliest predicted mean Julian date of spawn (208, 211, and 218, respectively). Due to the early spawning and high growth of YOY, these locations experienced the lowest amount of overwinter mortality in a given year (mean proportion of overwinter cohort mortality = 0.42, 0.56, and 0.58). In contrast, many northern regions exhibited much later spawn dates (e.g., St. Louis River, Lake Superior, mean Julian date of spawn = 246.5) and a much higher proportion of overwinter cohort mortality as a function of temperature (St. Louis mortality = 0.98). Some northern regions (e.g., Nipigon River in Lake Superior, Mississagi River in northern Lake Huron) experienced insufficient warming to initiate spawning activity. Each Great Lake exhibits at least one location where survival is expected to occur with high confidence. Furthermore, all sites where spawning was initiated have relatively high probability that at least one yearly cohort, out of all the cohorts hatched across a 20-year period, will survive the winter period on the basis of temperature ($P > 0.75$). Overwinter survival of YOY varies with location but establishment of Grass Carp in more northern latitudes is less probable given the general pattern of increasing overwinter mortality in northern regions.

INTRODUCTION

Year-class strength is determined during the early life stages in most fishes, so evaluating population dynamics during this time period provides insight into mechanisms that affect recruitment. Variation in year-class strength in natural populations of fish species, particularly those found near their northern limit, can be explained, in part, by temperature effects during the first summer and winter of life. While multiple factors interacting with temperature influence the degree of early mortality, temperature alone can be a strong driver of the overall survival of young-of-year (YOY) fishes under certain conditions (Shuter et al. 1980).

In temperate zones, there is pronounced seasonality to resource availability and, from south to north, the period of resource abundance shortens and the period of resource scarcity, associated with winter, lengthens (Shuter and Post 1990). During winter, most temperate zone fishes undergo physiological changes that result in declining condition and depletion of energy reserves (Cunjak 1988). As temperature decreases, the activity of YOY declines and movement and feeding may cease at low water temperatures in winter (Shuter et al. 1980, Bauer and Schlott 2004). While overwinter mortality may result from hypothermia, predation, or extended periods of low dissolved oxygen (known as winterkill), mortality of YOY as a result of starvation typically occurs if the energy reserves attained prior to the onset of winter are inadequate to survive the duration of the first winter (Holm et al. 2009).

The ability to withstand starvation is constrained by the same size-dependent effects that shape the metabolic functions of most organisms, with weight-specific basal metabolic rate increasing as fish size decreases (Shuter and Post 1990). Most studies of fat dynamics in fishes have shown that larger fishes also have higher initial lipid contents, with a positive relationship between body size and weight-specific fat content (Shuter et al. 1980, Henderson et al. 1988, Shuter and Post 1990, Thompson and Bergersen 1991). Thus, larger fishes can withstand winter starvation better than smaller fishes because of proportionally greater stored energy reserves and because high metabolic demands of small age-0 fishes exhaust energy supplies more quickly during winter, making smaller fishes less tolerant of starvation conditions (Shuter et al. 1980, Shuter and Post 1990). This phenomenon dictates a critical length that fish must attain prior to the onset of winter, or else death will occur as a result of starvation due to insufficient energy reserves. Therefore, the longer the duration of winter, the greater the critical length that must be attained prior to the onset of winter.

In temperate populations, numerous factors influence the size distribution that fishes attain prior to the onset of winter. Most of these factors are dependent to some degree on water temperature: onset of spawning, spawning duration, early development rate (hatching time), daily growth, and timing of the onset of winter. Fish size going into the first winter may be maximized by early onset of spawning, optimal water temperatures for maximal growth rate of YOY, and a prolonged growing period for YOY. Each of these factors influence the likelihood of overwinter survival, as fish size at the start of winter and overwinter survival are correlated.

Grass Carp (*Ctenopharyngodon idella)* is a sub-tropical to temperate species native to the large rivers of eastern Asia, where it tends to inhabit lower and middle reaches of rivers and connected lacustrine habitats (Cudmore and Mandrak 2004). Its range extends across latitudes 25–65°N and from coastal waters inland. Grass Carp was originally brought to North America in 1963 to evaluate its potential for biological control of aquatic vegetation. By the early 1970s, Grass Carp had escaped and entered the rivers of the central United States (Mitchell and Kelly 2006) posing a potential ecological threat to these systems and surrounding waterbodies.

Grass Carp has since established through much of the Mississippi River basin and numerous Grass Carp captures have since occurred in the Great Lakes basin (Mitchell and Kelly 2006, USGS Nonindigenous Aquatic Species (NAS) 2015). Concern over the risk Grass Carp pose to the Great Lakes basin has prompted an ecological risk assessment to assess the extent to which Grass Carp may arrive, survive, establish, spread, and the magnitude of ecological consequences it may cause. The establishment of Grass Carp in the Great Lakes basin is, in part, dependent upon the survival of early life stages. Because YOY overwinter mortality is correlated to length of winter, overwinter mortality is likely to become a more important mechanism of mortality with increasing latitude.

Overwinter mortality of YOY Grass Carp is not known to be biologically limiting in tributaries to southern Lake Erie and the Chicago-Area Waterway System, as diploid Grass Carp captured from the Lake Erie basin exhibited otolith microchemistry that was consistent with natural reproduction in the basin (Chapman et al. 2013, Whitledge 2014). However, it remains unclear as to the extent to which Grass Carp establishment may be limited by overwinter mortality of YOY in other regions of the Great Lakes basin, especially at northern latitudes.

Using an approach based on Shuter et al. (1980), we modelled the size-selective overwinter mortality of YOY Grass Carp for various locations in the Great Lakes basin. We estimated the critical lengths of Grass Carp necessary to survive the duration of winter, as well as the proportion of the YOY-length distribution that dies overwinter (cohort mortality) for localities within each of the Great Lakes. The model has two main components. First, we compiled statistics from the literature about temperature-specific biological attributes of the species, such

as the temperature at which spawning is initiated, the length of individuals at hatch, and daily growth of YOY as a function of temperature. These values were used to generate a biological baseline for YOY growth and were obtained from observed characteristics of populations beyond the basin because no such data exist for this specific area. Secondly, we compiled Great Lake-specific water temperature regimes and incorporated the biological characteristics within a general growth model to understand the extent of YOY survival as a function of length at a series of sites throughout the basin. Because we incorporate the variation in the natural temperature regimes of nearshore habitats or tributaries of the Great Lakes basin (two locations per lake: a 'southern' and 'northern' representative, where possible), results provide guidance on the approximate thermal limits to YOY survival as a function of overwinter mortality within each lake.

METHODS

The model was parameterized using biological values (onset of spawning, duration of spawning, hatching time, length at hatch, onset and end of winter, larval growth rate, and length-weight relationship) from literature and, where relevant, emphasis was placed on obtaining values that were derived from temperature conditions similar to the Great Lakes.

Once mature, Grass Carp require a minimum number of annual degree days (ADD) above 15 °C for onset of spawning that ranges 565–650 ADD15, and up to 919 ADD15 for mass spawning (Gorbach and Krykhtin 1980, 1981, Bogutskaya et al. 2017). Gorbach and Krykhtin (1981) reported 633 ADD15 and a water temperature that is >17 °C for spawning onset for Grass Carp (Kocovsky et al. 2012), which is an intermediate value to the estimated range and was subsequently used in our model. The duration of spawning was estimated based on the duration of spawning from similar habitats reported in the literature. Studies from Russia, Turkmenistan, U.S., and China were included and ranged from ~42 to 90 days (Shireman and Smith 1983, Hargrave and Gido 2004, Chapman et al. 2013, Bogutskaya et al. 2017). Chapman et al. (2013) noted the approximate onset of spawning in Lake Erie to be June 23, 2012 and the end of the spawning season to be September 15, 2012, when water temperatures fell below 18 °C (lower limit of Asian carp spawning, Kolar et al. 2007); a duration of 84 days. We used a mean spawning duration of 50 days, unless temperatures fell below 18 °C (which would terminate spawning). In general and for a given date of spawn initiation, a longer spawning season should not lead to a greater proportion of individuals surviving the duration of winter, because later-hatched fish will occupy the smaller portion of the fall length distribution. We used an egg incubation time, or hatching time (time from fertilization to hatching) of 1 day, which was estimated based on George and Chapman (2015) development rates for Grass Carp at an experimental temperature range of 19–23°C. If water temperatures drop below 13.5 °C or exceed 27 °C during the incubation period, then 100% mortality was deemed to occur (Kolar et al. 2007, Deters et al. 2013, George and Chapman 2015). We used a total length (TL) at hatch of 6 mm for Grass Carp based on Yi et al. (2006).

The linear relationship between daily growth rate in length (cm/day) and daily temperature (°C) for YOY Grass Carp was generated from literature sources (n = 5; Inaba et al. 1957 as cited in Shireman and Smith 1983, Maceina and Shireman 1980, Brown and Coon 1991, Yi et al. 2006, Zhang et al. 2012) and is represented by the following formula:

$y = -0.23 + 0.016^{*}x$,

where y is the daily growth in centimeters and x is the average daily water temperature. This relationship was used to construct daily growth increments from the length at first hatch through to the onset of winter (i.e., the beginning of the period where 8 °C is reached) and is, hereafter, referred to as the length-frequency distribution of the fall cohort. Because daily growth was

calculated and tracked for each of the spawning days (n = 50), the distribution of fish lengths leading into the fall had a maximum of 50 values, although fewer values may have occurred when poor hatch conditions were encountered. The histogram of 50 values represents the distribution of fish lengths following their cumulative daily growth and provide the relative abundance of each length class (assuming a constant number of fish 'hatched' per day) that will exist at the onset of winter (i.e., we do not incorporate real variation in the number of fish actually produced during each of the 50 days of hatching, but rather place a single 'fish' for that day in a single length bin).

To estimate the critical length that must be attained for YOY to survive the winter, which is a function of the duration of winter period as well as metabolic factors, we used base metabolic rates that were developed for YOY Smallmouth Bass (*Micropterus dolomieu*) and presented in Shuter et al. (1980). Using a surrogate species was necessary because even with a Grass Carp- specific metabolic rate, the weight loss leading to starvation and death in YOY Grass Carp is unknown. Therefore, our approach involves spawning, hatching, and daily growth specific to Grass Carp with values derived from the literature, but assumes that YOY Grass Carp metabolize reserve energy at the same rate as YOY Smallmouth Bass during winter. From Shuter et al. (1980), the initial ash-free dry weight (AFDW)-length relationship was used to relate the lengths of the fall Grass Carp YOY cohort to the availability of energy at the onset of the winter period. A second relationship describing the critical availability of energy involved the AFDW for length at which death occurs. Thus, the daily metabolic rate, expressed per day, can be used in relation to the duration of winter to understand if sufficient reserve energy has been attained during the growth period. The value of critical length (L_{crit}) represents the theoretical length that YOY Grass Carp must reach to survive the duration of winter and is a function of both the duration of winter and the daily metabolic rate from Shuter et al. (1980).

Literature describing feeding activity of Grass Carp was compiled to identify the temperature threshold at which feeding ceases. Grass Carp fry were reported to not feed at temperatures below 8 °C (Shireman and Smith 1983), while the threshold temperature for onset of feeding for diploid Grass Carp was estimated at 10 °C (Wiley and Wike 1986). In another review, Grass Carp were noted to rarely feed at temperatures below 3 °C; between 3 and 6 °C, they may feed at intervals of 5–7d (Chilton and Muoneke 1992); in overwinter habitat they were reported to not feed at all (Cudmore and Mandrak 2004); and, steady consumption was reported to start at 10–16 °C (Shireman and Smith 1983). Pípalová (2006) reviewed the literature and reported feeding to stop at water temperatures below 16 °C. In Alberta, studies suggest that Grass Carp have moderate feeding activity between 13 °C and 18 °C and limited feeding below 13 °C (Ackenberry Trout Farms 2015). Given the variation in studies involving the relationship between temperature and feeding activity of Grass Carp, we chose a conservative estimate for the onset and end of winter, calculated as the period where water temperature reaches 8 °C or lower. The 8 °C threshold represents the temperature in the model below which consumption and growth ceases and can be expressed as the number of days in a calendar year ('length of winter' in the remainder of this document).

Year-round water temperature data were obtained for each of the Great Lakes from various sources (USGS 2015; Y. Zhao, Ontario Ministry of Natural Resources and Forestry (OMNRF), pers. comm.; L. Witzel, OMNRF, pers. comm.; Fisheries and Oceans Canada, Sea Lamprey Control Centre, unpubl. data) (Table 3.1). Multiple years of data were obtained (10 most recent continuous years of data, or as many as were available) and, for most stations a minimum of 5 temperature measures were taken throughout a given day.

Table 3.1. Summary of daily water temperature series obtained for localities throughout the Great Lakes basin.

Lake	Location	Duration	Reference
Lake Superior	Nipigon River	1996–2010	Fisheries and Oceans Canada (DFO), Sea Lamprey Control Centre (SLCC)
Lake Superior	St. Louis River	2011–2014	USGS National Water Information System (Station 04024000)
Lake Huron	Mississagi River	2010–2014	DFO, SLCC
Lake Huron (Georgian Bay)	Still River	2004–2005	DFO, SLCC
Lake Huron	Saginaw River	2012–2014	USGS National Water Information System (Station 04157005)
Lake Michigan	Fox River, Green Bay	2012–2014	USGS National Water Information System (Station 040851385)
Lake Michigan	Portage–Burns Waterway	2011–2012	USGS National Water Information System (Station 04095090)
Lake Erie	Big Creek	2001–2009, 2012, 2013	DFO, SLCC
Lake Erie	Long Point, Inner Bay (Bait Island)	2005–2008	OMNRF
Lake Erie	Port Dover (nearshore)	2006–2008, 2011–2012	OMNRF
Lake Erie	Vermillion River	2012–2014	USGS National Water Information System (Station 04199500)
Lake Ontario	Humber River	1999–2003, 2005–2009, 2011–2013	DFO, SLCC
Lake Ontario	Genesee River	2011–2013	USGS National Water Information System (Station 04231600)
Lake Superior	Nipigon River	1996–2010	DFO, SLCC

Locations were selected to represent a 'southern' and 'northern' region of each Great Lake and all locations were chosen from the lower reaches of U.S. and Canadian tributaries (<10 km from mouth of lake) or from nearshore areas within the Great Lake proper (Figure 3.1). In Lake Huron, an extra location (Still River) was selected to represent Georgian Bay, which may have a different temperature regime compared with Lake Huron (Figure 3.1). In addition, two nearshore localities were also selected for Lake Erie (Inner Bay near Bait Island, and Port Dover) to determine if the spawning and early growth in the Great Lakes proper would result in different

estimates of overwinter mortality compared to those from nearby tributary locations (Figure 3.1). Mean daily water temperature for each location was derived for each year of data (e.g., the daily average was calculated from multiple temperature values in a single day), providing several yearly water temperature sets for each location.

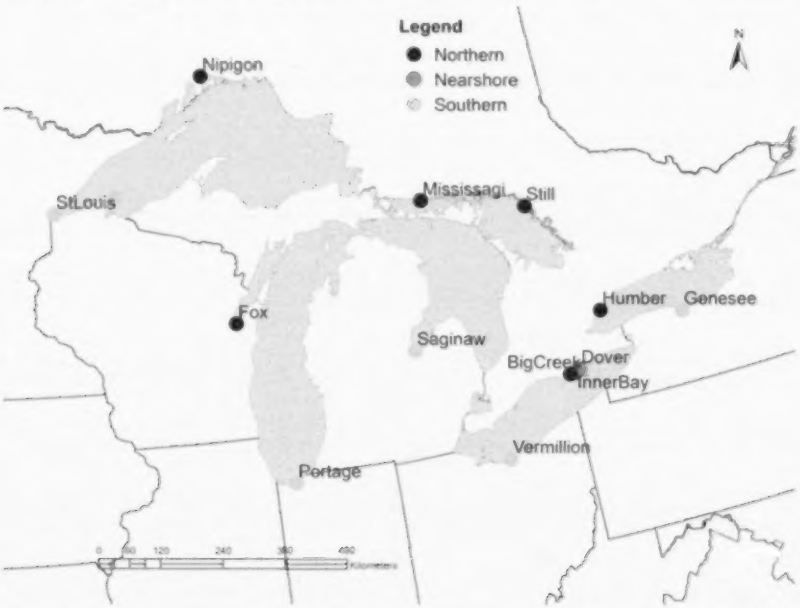

Figure 3.1. Locations for which multiple years of water temperature data were available in the Great Lakes basin.

For each geographic location in each lake, we conducted a series of stochastic simulations that incorporated uncertainty in temperature regime and daily growth to understand the resulting distributions of overwinter mortality, critical lengths, and the Julian date of the onset of spawning activity. We conducted 1,000 iterations per geographic location, which began by randomly selecting a single yearly set of mean daily water temperatures. With this single temperature series, we calculated the onset of spawning activity, plus hatch time and length at hatch. We then incorporated uncertainty in the relationship between daily growth increment and temperature by sampling values from a uniform distribution of the 95% CI of the slope and intercept of the daily growth-temperature relationship. This approach allowed expected daily growth to vary realistically, given uncertainty in the original daily growth-temperature regression that was derived from the literature. We then calculated the fall cohort length distribution for this single iteration, including the fraction of the length distribution that surpasses the value of L_{crit}. This approach allowed overwinter mortality as a function of length (a value between 0 and 1, representing the proportion of the fall cohort that fails to surpass L_{crit}) to be calculated for a single year. The process was repeated 1,000 times (e.g., 1,000 temperature regimes with different outcomes of growth). This simulation provided a total of 1,000 critical lengths (due to different durations of winter), allowing the mean and 95% value of L_{crit} to be generated. A total of 1,000 values were also obtained for the Julian date at first spawn and cohort mortality, allowing the mean and 95% confidence limits to be recorded for these values. Because cohort mortality represents the proportion of the length distribution failing to survive, we also calculated the overall probability of survival for a single year, which was derived as the number of simulations in which survival occurs (i.e., mortality < 1.0), divided by the total number of yearly trials. The yearly probability of survival value was extended with a binomial probability calculation to

determine the overall probability of survival across 5-, 10-, and 20-year time periods. This survival calculation is based on temperature effects only and does not take into account the variation in the abundance of the daily cohort or other factors (e.g., predation) known to influence mortality in natural populations. The general structure of the model was as follows: spawning is initiated based on warming temperatures, spawning window continues for 50 days, producing ~ 50 daily cohorts, hatched fish attain a given length prior to the onset of winter based on the daily temperature series, and fish either survive or fail to survive overwinter based on the duration of winter (Figure 3.2).

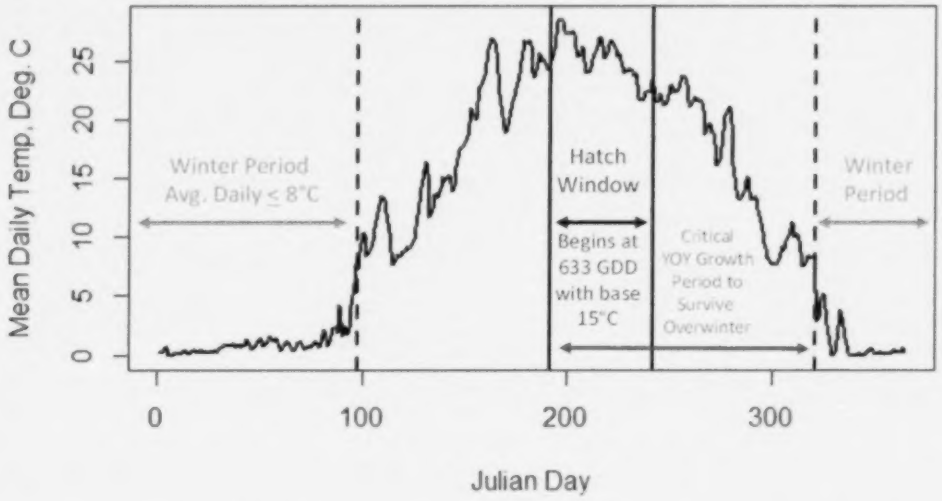

Figure 3.2. Schematic of the timing and duration for key biological stages for overwinter survival of YOY Grass Carp. Shown is the 2009 daily temperature series for the nearshore region of Long Point, Lake Erie (Inner Bay).

Sensitivity analysis was performed to determine the influence of specific parameters on the degree of overwinter mortality. We incorporated three parameters within the sensitivity analysis:

1) the number of degree-days required for spawning to initiate (modeled as a 25% decrease over baseline);
2) the slope of the daily growth-temperature regression (modeled as a 25% increase over baseline); and,
3) the length at first hatch (modeled as a 25% increase over baseline).

We initially explored the influence of increasing the spawn and hatch windows, but these simulations produced only minor changes in overwinter mortality.

RESULTS

Mean daily water temperatures indicated a range of temperature regimes across the locations of interest (Figure 3.3). Generally, northern latitudes had coolest temperatures with the greatest duration of winter, such as the Nipigon River in Lake Superior, which is noticeably colder throughout the year and takes substantially longer to begin warming (Figure 3.3). The warmest location, as indicated by a sharp rise in spring temperature, high maximum temperature, and short duration of winter, was Portage-Burns Waterway, Lake Michigan. Other notable results were relatively cool daily temperatures in Big Creek, Lake Erie (seen as the coolest of the Lake

Erie series with low daily average temperatures throughout summer; Figure 3.3), as well as same-lake tributary variability, such as the relatively cool temperatures of Mississagi River and Still River relative to Saginaw River in Lake Huron (Figure 3.3).

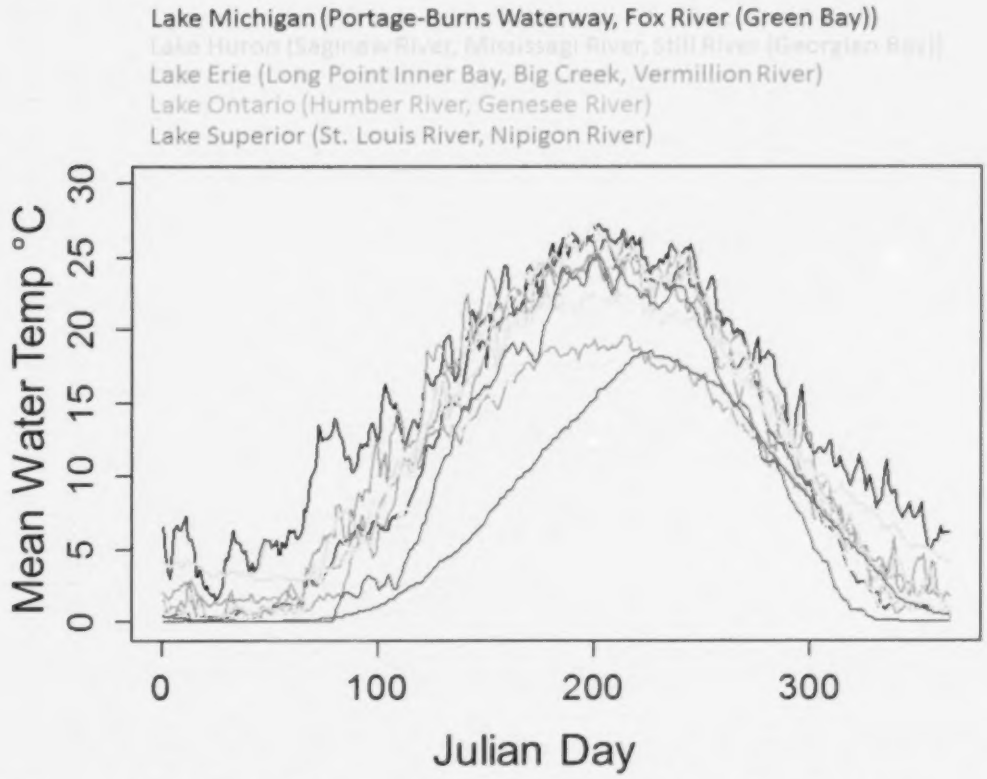

Figure 3.3. Grand mean (mean daily temperatures over multiple years) daily temperature values for nearshore and tributary locations throughout the Great Lakes basin used to estimate overwinter mortality.

Model results revealed that the average critical size (L_{crit}) of Grass Carp at onset of winter differed between lakes and between locations within lakes (Table 3.2, Figure 3.4), as did the onset of spawning, duration of winter, cohort mortality and probability of survival (Table 3.3 and 3.4; Figure 3.4).

Table 3.2. Summary of the critical length (L_{crit}; cm) required for Grass Carp to survive the overwinter period in locations throughout the Great Lakes basin. Also shown is the grand mean of fall length attained, based on an average of 1,000 simulations derived from multiple years of temperature data. Values of 0 for grand mean fall lengths indicated that spawning activity failed to be initiated under all temperature regimes. Locations are listed with northern locations followed by southern locations.

Location	L_{crit} (cm)	L_{crit} (Lower 95 CI; cm)	L_{crit} (Upper 95 CI; cm)	Grand Mean Fall Length (cm)	Grand Mean Fall Length (Lower 95; cm)	Grand Mean Fall Length (Upper 95; cm)
Superior						
Nipigon River	7.03	6.8	7.5	0	0	0
St. Louis River	6.47	6	6.7	1.26	0.6	6.37
Huron						
Mississagi River	6.05	5.9	6.2	0	0	0
Still River	6.35	6.3	6.4	0.001	0	0
Saginaw River	5.64	5	6	6.69	0.62	28.04
Michigan						
Fox River	5.71	4.9	6.2	6.34	0.62	27.38
Portage River	3.75	3.6	3.9	9.83	0.63	37.96
Erie						
Big Creek	5.65	5	6.2	0.01	0	0
Long Point Inner Bay	5.62	5.3	6	5.87	0.62	25.6
Port Dover Nearshore	5.55	5.3	5.9	0.34	0	3.73
Vermillion River	5.08	4.6	5.4	6.85	0.62	28.3
Ontario						
Humber River	5.22	4.5	5.9	2.39	0	14.52
Genesee River	5.41	4.9	5.8	6.65	0.61	27.4

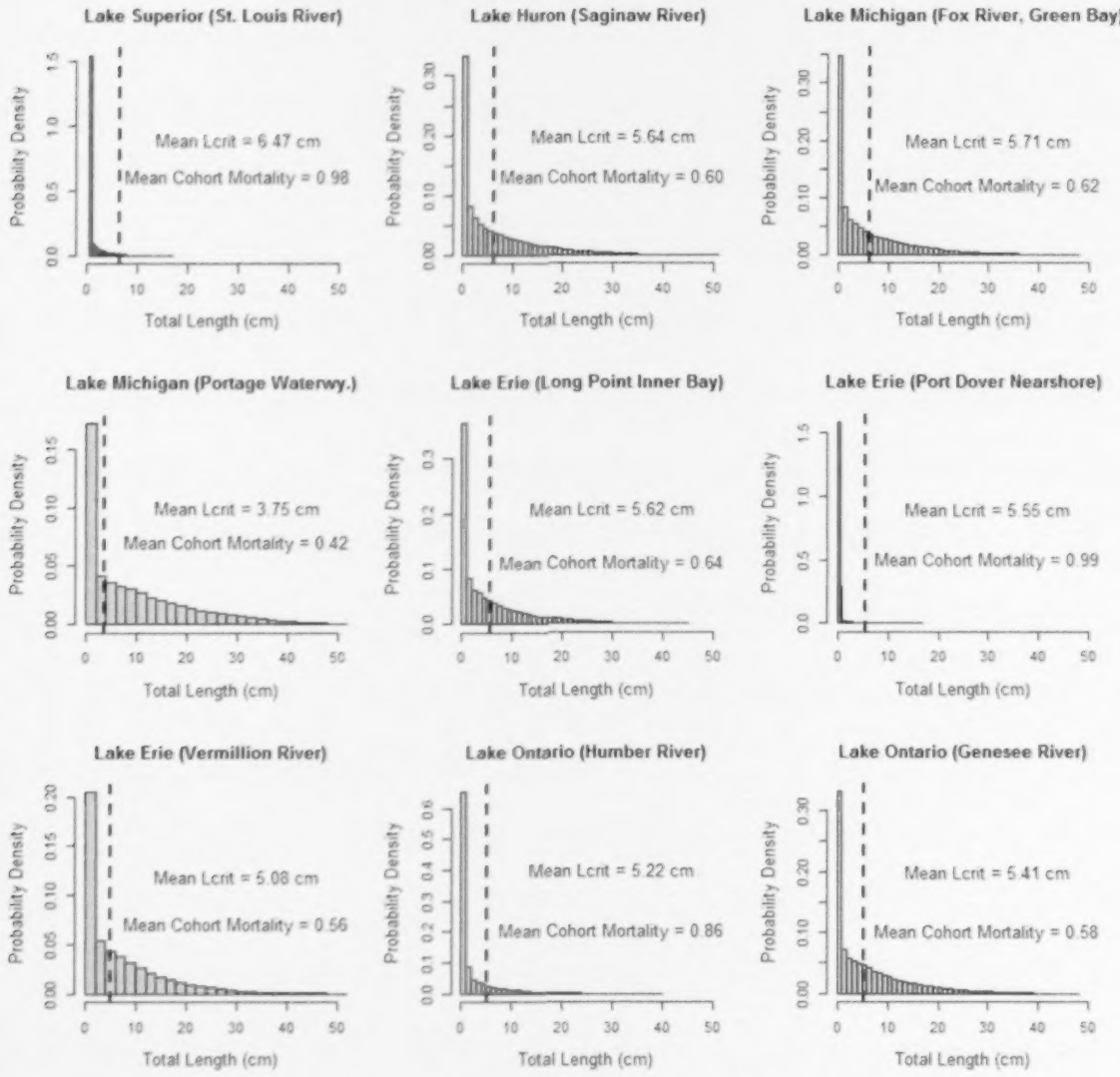
Lake Superior (St. Louis River)
Mean Lcrit = 6.47 cm
Mean Cohort Mortality = 0.98
Lake Huron (Saginaw River)
Mean Lcrit = 5.64 cm
Mean Cohort Mortality = 0.60
Lake Michigan (Fox River, Green Bay)
Mean Lcrit = 5.71 cm
Mean Cohort Mortality = 0.62
Lake Michigan (Portage Waterwy.)
Mean Lcrit = 3.75 cm
Mean Cohort Mortality = 0.42
Lake Erie (Long Point Inner Bay)
Mean Lcrit = 5.62 cm
Mean Cohort Mortality = 0.64
Lake Erie (Port Dover Nearshore)
Mean Lcrit = 5.55 cm
Mean Cohort Mortality = 0.99
Lake Erie (Vermillion River)
Mean Lcrit = 5.08 cm
Mean Cohort Mortality = 0.56
Lake Ontario (Humber River)
Mean Lcrit = 5.22 cm
Mean Cohort Mortality = 0.86
Lake Ontario (Genesee River)
Mean Lcrit = 5.41 cm
Mean Cohort Mortality = 0.58
Probability Density
Total Length (cm)

Figure 3.4. Overall length-frequency distributions of the fall cohort at the onset of winter, derived by aggregating 1,000 permutations of yearly temperature regimes and daily growth increments. The dashed vertical line represents the mean L_{crit} (e.g., length that must be attained to survive overwinter). Length classes to the left side of the dashed line are predicted to die as a result of starvation; length classes to the right side of the dashed line have attained sufficient reserves to persist past the winter starvation period. Locations where spawning failed to initiate are not shown.

Table 3.3. Summary of the Julian date of the initiation of the spawning period, based on a temperature cue of 633 ADD 15. Also shown is the duration of winter, which was calculated as the number of days following the Julian date of first spawn that are ≤ 8 °C. Locations are listed with northern locations followed by southern locations.

Location	Julian Spawn Date (mean)	Julian Spawn Date (lower 95% CI)	Julian Spawn Date (upper 95% CI)	Length of Winter (# of days ≤ 8 °C)	Length of Winter Lower 95 (# of days ≤ 8 °C)	Length of Winter Upper 95 (# of days ≤ 8 °C)
Superior						
Nipigon River	0	0	0	215.8	205	235
St. Louis River	246.5	236	253	193.5	175	204
Huron						
Mississagi River	0	0	0	177.8	172	184
Still River	0	0	0	188.9	188	190
Saginaw River	213.6	201	222	160.3	137	174
Michigan						
Fox River	219.6	205	227	163.7	133	182
Portage River	208.2	196	220	93.5	88	99
Erie						
Big Creek	0	0	0	161.1	138	181
Long Point Inner Bay	221.4	217	230	159.9	147	175
Port Dover Nearshore	251	0	251	157.2	146	171
Vermillion River	211.4	193	222	139.7	123	152
Ontario						
Humber River	243.3	0	276	145	117	171
Genesee River	218.3	209	225	151.4	133	166

Table 3.4. Summary of overwinter cohort mortality and corresponding probability of survival (as a function of temperature) at 1, 5, 10, and 20 year time periods. Locations are listed with northern locations followed by southern locations.

Location	Mortality (mean)	Mortality (lower 95% CI)	Mortality (upper 95% CI)	P Survival (1 Year)	P Survival (5 Years)	P Survival (10 Years)	P Survival (20 Years)
Superior							
Nipigon River	1	1	1	0	0	0	0
St. Louis River	0.98	0.76	1	0.17	0.61	0.85	0.98
Huron							
Mississagi River	1	1	1	0	0	0	0
Still River	1	1	1	0	0	0	0
Saginaw River	0.6	0	1	0.55	0.98	0.99	0.99
Michigan							
Fox River	0.62	0	1	0.56	0.98	0.99	0.99
Portage River	0.42	0	1	0.68	0.99	0.99	1
Erie							
Big Creek	1	1	1	0	0	0	0
Long Point Inner Bay	0.64	0	1	0.53	0.98	0.99	0.99
Port Dover Nearshore	0.99	0.76	1	0.07	0.29	0.50	0.75
Vermillion River	0.56	0	1	0.58	0.99	0.99	0.99
Ontario							
Humber River	0.86	0.04	1	0.34	0.88	0.98	0.99
Genesee River	0.58	0	1	0.59	0.99	0.99	0.99

Lake Superior

Mean L_{crit} was 7.03 (Nipigon River; northern Lake Superior tributary) and 6.47 (St. Louis River; southern Lake Superior tributary) (Table 3.2). However, based on multiple years of temperature data, spawning was not initiated in the Nipigon River (i.e., 633 ADD 15 was not reached). In the St. Louis River, the mean Julian date of spawn was 246 (September 3) at a value of 633 ADD 15 (Table 3.3). Despite the late spawning, St. Louis River populations did attain sufficient length for a fraction of the fall cohort to survive overwinter in some years, although average mortality values were high (0.98, 95% CI between 0.78 and 1; Table 3.4, Figure 3.4). Taken over a 20-year time period, the probability of YOY surviving overwinter in the St. Louis River was high (P = 0.97; Table 3.4).

Lake Huron

Mean L_{crit} was 6.05 cm (Mississagi River; northern Lake Huron tributary) and 5.64 cm (Saginaw River, southern Lake Huron tributary, and was 6.35 cm for Georgian Bay (Still River) (Table 3.2). In both the Mississagi River and Still River, spawning failed to occur due to insufficient temperatures, but in the Saginaw River the mean Julian date of spawning was 213 (August 1) (Table 3.3). Only Saginaw populations attained sufficient length for a sizable fraction of the fall cohort to survive overwinter (mean overwinter mortality = 0.6; Table 3.4; Figure 3.4). Taken over a 20-year time period, the overall probability of YOY surviving overwinter in the Saginaw River was high (P = 0.99; Table 3.4).

Lake Michigan

Mean L_{crit} was 5.71 (Fox River; northern Lake Michigan tributary in Green Bay) and 3.75 (Portage-Burns Waterway, southern Lake Michigan tributary) (Table 3.2). In both cases, the low L_{crit} values reflected the shorter duration of winter compared with Lake Superior tributaries. In the Fox River, the mean Julian date of spawn was 219 (August 7), whereas mean Julian date of spawn was 208 (July 27) for the Portage-Burns Waterway (Table 3.3). Both populations attained sufficient length for a sizable fraction of the fall cohort to survive overwinter (mean overwinter mortality = 0.62 for Fox River and 0.42 for the Portage-Burns Waterway; Table 3.4, Figure 3.4). Taken over a 20-year time period, the overall probability of YOY surviving overwinter in both systems was high (P = 0.99, Fox River, P = 1.0, Portage-Burns Waterway; Table 3.4).

Lake Erie

Mean L_{crit} was 5.65 cm (Big Creek, northern Lake Erie tributary) and 5.08 (Vermillion River; southern Lake Erie tributary; Table 3.2). Values for two additional locations were calculated in the Long Point Bay area to reflect a scenario for open-water spawn initiation and associated overwinter survival. Mean L_{crit} was 5.62 cm in nearshore Long Point Bay (Inner Bay, near Bait Island, northern shore of Lake Erie) and was 5.55 cm in the nearshore waters of Port Dover (depth of ~ 3 m; northern shore of Lake Erie). In the Vermillion River, the mean Julian date of spawn was 211 (July 30), whereas, mean Julian date of spawn was 221 (Long Point Bay, August 9) and 251 (Port Dover; September 8, but see a 95% CI containing a value of 0, indicating spawning failure in many years in Port Dover). Spawning always failed to occur in Big Creek, likely as a result of substantial groundwater influence leading to cool summer temperatures in that system. The remaining populations attained sufficient length for survival overwinter (mean overwinter mortality = 0.56 for Vermillion River, 0.64 for Long Point, and 0.99 for Port Dover nearshore; Table 3.4, Figure 3.4). Taken over a 20-year time period, the overall probability of YOY surviving overwinter was high (Vermillion River and Long Point, P = 0.99, Port Dover nearshore, P = 0.75; Table 3.4).

Lake Ontario

Mean L_{crit} was 5.22 (Humber River; northern Lake Ontario tributary) and 5.41 (Genesee River, southern Lake Ontario tributary; Table 3.2) and the temperature cue to spawn was reached in both systems. In the Humber River, the mean Julian date of spawn was 243 (August 31), whereas, mean Julian date of spawn was 218 (August 6) for the Genesee River (Table 3.3). Both populations attained sufficient length for a fraction of the fall cohort to survive overwinter (mean overwinter mortality = 0.86 for Humber River and 0.58 for the Genesee River; Table 3.4, Figure 3.4), with probabilities above P = 0.99 for overwinter survival over a 20-year period (Table 3.4).

Basin-wide sensitivity analysis

Sensitivity analysis revealed that the slope of the daily growth increment-temperature relationship had the greatest influence on overwinter mortality, relative to changes in the number of growing degree days required to initiate spawn or hatch length. While overwinter mortality changed in response to shifts in all input parameter values, such changes resulted in less than 25% changes in overwinter mortality, indicating that the model is relatively robust to shifts of those parameters (Figure 3.5).

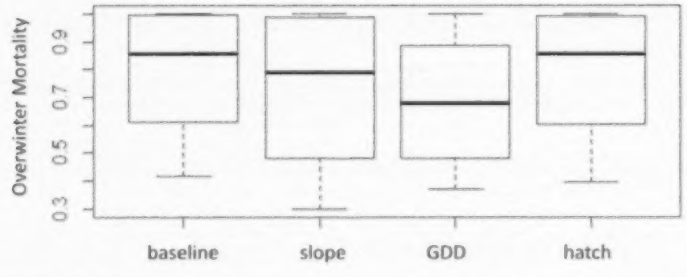

Figure 3.5. Results of sensitivity analysis. Values within each boxplot (n = 11 values per boxplot) are the mean proportion of overwinter mortality for each location under a baseline scenario (parameters held at status quo), and the values in overwinter mortality resulting from a 25% increase in the slope of the daily increment-temperature relationship ("slope"), a 25% decrease in the number of annual degree days to initiate spawning ("ADD"), and a 25% increase in the size at hatch ("hatch").

Although validating our overwinter model is difficult without observing spawning, growth, and mortality of Grass Carp within the basin, the fall cohort length distributions produced in this model for southern Erie populations (95% CI of all lengths = 0.62 cm, 28.3 cm for Vermillion River) exhibited values that are consistent with back-calculated length at the end of the first growing season for Grass Carp caught in the tributaries of lakes Michigan and Erie (Chapman et al. 2013, USGS NAS 2015; P. Kocovsky, USGS, pers. comm.).

CONCLUSION

Overwinter survival of Grass Carp is predicted to occur in each Great Lake, although substantial variability exists within lakes as a function of differences in temperature regimes. Failure to spawn as a function of temperature is an important driver in northern Lake Huron (Mississagi River, Still River) and in northern Lake Superior (Nipigon River), and is also suspected to be relevant in systems with high groundwater influence (e.g., Big Creek, Lake Erie). Despite a high fraction of cohort mortality in a given year, all populations that initiated spawning exhibited relatively high ($P \geq 0.75$) probabilities that at least one cohort, out of a group of cohorts hatched across a 20-year period, will survive within the Great Lakes.

GENERAL CONCLUSIONS

The research papers presented here in support of the Grass Carp (*Ctenopharyngodon idella*) risk assessment used modelling approaches to predict that under current lake conditions, survival, growth and establishment of Grass Carp in the Great Lakes basin is possible. More specifically, the following main summary points are:

Bioenergetics modelling of potential growth and consumption

- Growth and survival in the Great Lakes is possible using a variety of diets including solely *Cladophora*.
- The impacts of a sustained breeding population are predicted to be large with adult individuals consuming up to 90 kg of macrophytes annually.
- These impacts could be amplified if feeding preference or foraging behaviour results in plant damage beyond what is consumed.

Establishment

- Using point estimates, the net reproductive rate for Grass Carp in the Great Lakes is 24.8, indicating that with our best available information, Grass Carp is likely to establish in the Great Lakes.
- Even with uncertainty considered, over 90% of the estimates had $R_0 > 1$, indicating that under some environmental conditions that directly influence survival or reproduction, some introductions efforts may fail, but the preponderance of evidence from the literature indicates that Grass Carp are likely to become established if introduced to the Great Lakes.

Overwinter survivorship of YOY

- Overwinter survival of Grass Carp is predicted to occur in each Great Lake; although substantial variability exists within lakes as a function of differences in temperature regimes.
- Despite a high fraction of cohort mortality in a given year, all populations that initiated spawning exhibited relatively high ($P \geq 0.75$) probabilities that at least one cohort, out of a group of cohorts hatched across a 20-year period, will survive within the Great Lakes.

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APPENDIX 1: DISTRIBUTION OF GRASS CARP INTO SUITABLE STREAMS

There is a concern that an aggregation of Grass Carp into a stream is needed to instigate a reproductive event. With multiple streams in the Great Lakes, some with characteristics suitable to support Grass Carp recruitment but others without, there is the potential that aggregation of sufficient Grass Carp would not occur without a substantial population of adults in the Great Lakes. Currently there is little information to guide our understanding of Grass Carp aggregation behaviour, but we can use a probabilistic exercise to guide discussions and considerations of potential Grass Carp establishment due to low densities of Grass Carp requiring aggregations in streams capable of supporting Grass Carp recruitment.

There are many rivers and streams in each of the Great Lakes, k, some are suitable for juvenile Grass Carp recruitment. The probability of being suitable for Grass Carp recruitment will vary between lakes, but let it be denoted as p_s. On average, from a binomial distribution we expect there to be $k*p_s$ suitable rivers and $k(1–p_s)$ unsuitable rivers for reproduction.

Now assume there are n Grass Carp in the system with an equal chance of entering a river to spawn, $1/k$. If fish cannot distinguish between rivers that do and do not allow for successful spawning, then the probability of an individual fish selecting a successful river for spawning is $p_r = (p_s/k)$ and can be treated as another binomial distribution,

$$\mathrm{p_r}(X = x) = \binom{n}{x}\left(\frac{p_s}{k}\right)^x\left(1 - \frac{p_s}{k}\right)^{n-x}$$

where the random variable X is the distribution of the number of reproductively viable Grass Carp in a stream potentially leading to a reproductive event. Because Grass Carp may need to aggregate to initiate spawning, a threshold value of a minimum number of fish may be desirable to estimate the risk of a spawning event. The probability of getting over a threshold number of fish is:

$$\mathrm{p_r}(X \geq x) = 1 - \sum_{x=0}^{M-1}\binom{n}{x}\left(\frac{p_s}{k}\right)^x\left(1 - \frac{p_s}{k}\right)^{n-x}$$

where M is a defined threshold of the minimum number of fish necessary to induce spawning.

Example: If we assume that any female Grass Carp will be capable of spawning, then our threshold would be very low, M = 1. Then the above equation reduces to $1 - \left(1 - \frac{p_s}{k}\right)^n$. We can look across the parameter space, $0 < p_s/k < 1$ and $n = 1, 2, 3, \ldots \infty$, at this function (Figure B.1). The figure shows that even if there are proportionally few streams in a system, (i.e., $p_s/k = 0.05$) capable of supporting reproduction, then the probability of at least one female finding a stream when there 15 female fish in the system is $1–(1–0.05)^{15} = 0.53$. In contrast, if there was a threshold of M = 2 or M = 3, then the probability would decrease to 0.17 and 0.026, respectively.

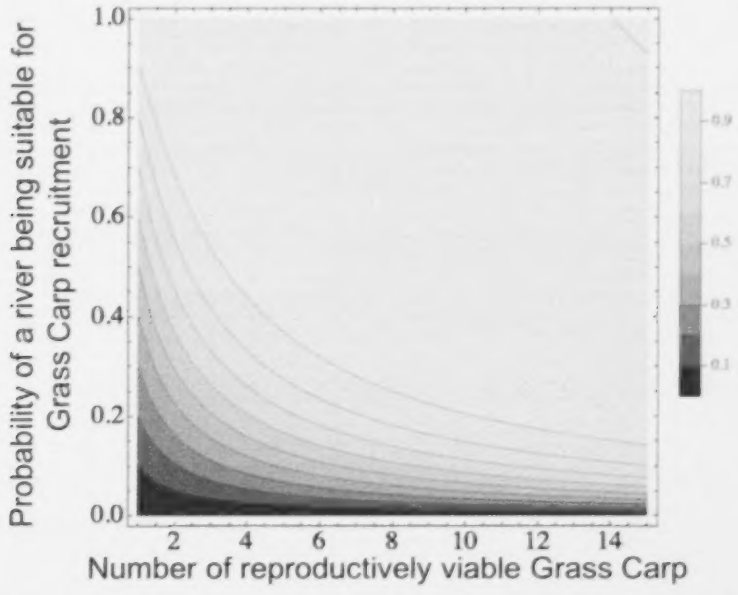

Figure B.1. Probability of at least one Grass Carp occurring in a suitable spawning tributary.

The four parameters critical to this exercise are the number of rivers potentially drawing Grass Carp in, the probability that any given river may support recruitment of any eggs once fertilized, the population size of Grass Carp in the system, and defining a threshold necessary to initiate a spawning event.